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PROCEEDINGS OF THE FAO CONFERENCE ON FISH BEHAVIOUR IN RELATION TO FISHING TECHNIQUES AND TACTICS

ACTES DE LA CONFÉRENCE FAO SUR LE COMPORTEMENT DU POISSON EN FONCTION DES TECHNIQUES ET TACTIQUES DE PÊCHE

ACTAS DE LA CONFERENCIA DE LA FAO SOBRE EL COMPORTAMIENTO DE LOS PECES EN RELACION CON LAS TECNICAS Y TACTICAS PESQUERAS

Bergen, Norway, 19-27 October 1967
Bergen, Norvège, 19-27 octobre 1967
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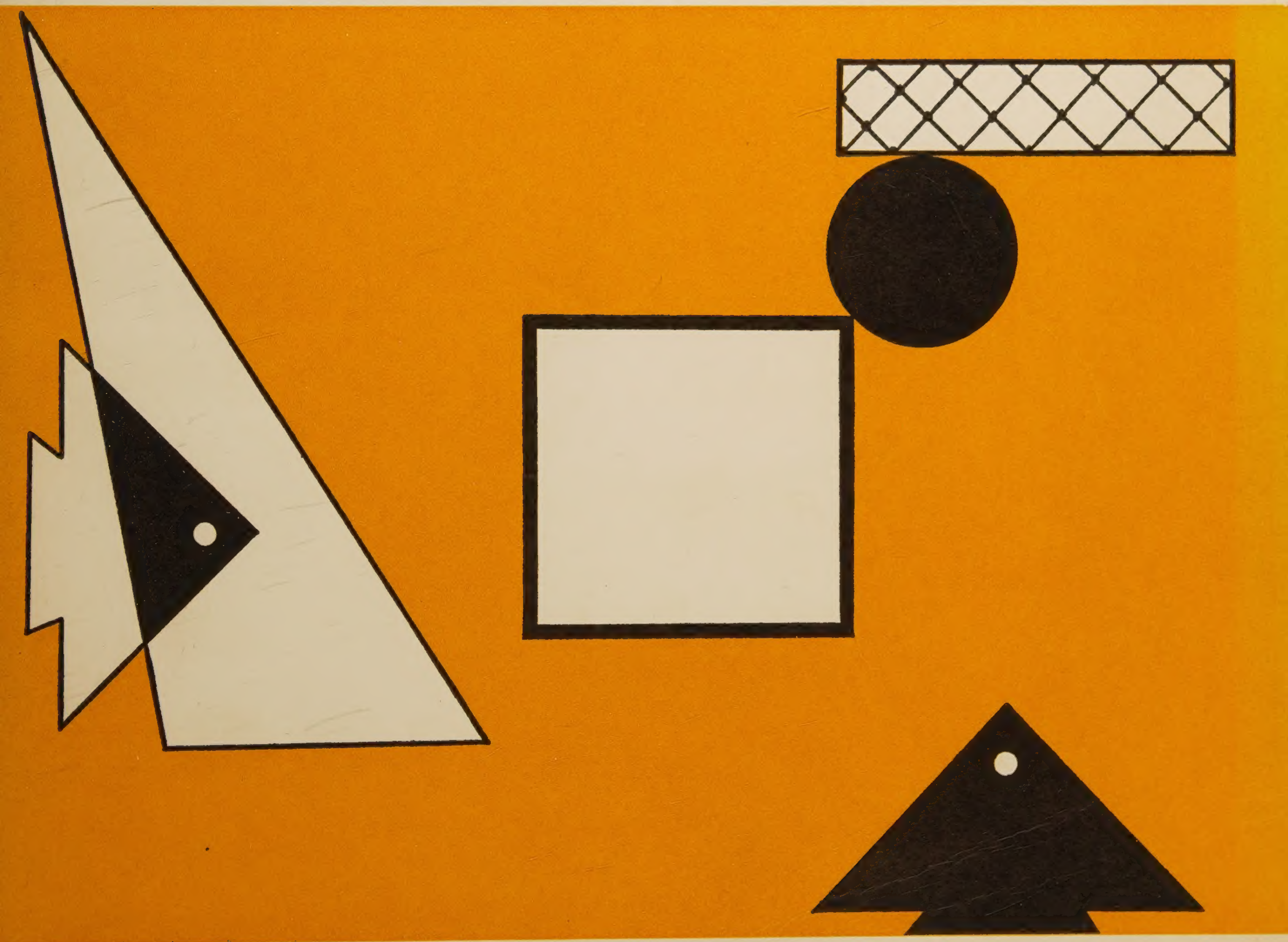

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VOLUME II - REVIEW AND EXPERIENCE PAPERS

VOLUME II - ETUDES SPECIALISEES ET COMPTES RENDUS D'EXPERIENCES

VOLUMEN II - DOCUMENTOS DE INFORMACION Y EXPERIENCIAS

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
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Rome, July 1969 Rome, juillet 1969 Roma, julio 1969

PREPARATION OF THIS VOLUME

This is the second volume of the Proceedings of the FAO Conference on Fish Behaviour in relation to Fishing Techniques and Tactics and contains the review papers and the first of the experience papers contributed to the Conference.

The first volume contains the report of the Conference, list of contributions and list of participants; the third volume contains the remaining experience papers.

The views expressed in the contributions are those of the authors and not necessarily of the Food and Agricultural Organization of the United Nations.

In addition to the editors the following persons helped to prepare this volume: Dr. (Mrs.) E. Clarke, Mr. S. Olsen and Biological Data Section, Fishery Resources and Exploitation Division.

PREPARATION DU PRESENT VOLUME

Ce tome est le second des Actes de la Conférence FAO sur le Comportement du Poisson en Fonction des Techniques et Tactiques de Pêche; il comprend les études spécialisées et les premiers comptes rendus d'expériences présentés à la Conférence.

Le premier tome comporte le rapport de la Conférence, la liste des contributions et celle des participants; le troisième tome comporte les autres comptes rendus d'expériences.

Les vues exprimées dans les contributions sont celles des auteurs et pas nécessairement celles de l'Organisation des Nations Unies pour l'alimentation et l'agriculture.

MM. E. Clarke et S. Olsen et la Section des données biologiques de la Division des ressources et de l'exploitation des pèches ont participé à la préparation du présent volume.

PREPARACION DE ESTE VOLUMEN

Este es el segundo volumen de las Actas de la Conferencia de la FAO sobre el Comportamiento de los Peces en Relación con las Técnicas y Tácticas Pesqueras y contiene los documentos de reseña y el primero de los de información que fueron presentados a la Conferencia.

El primer volumen contiene el informe de la Conferencia, lista de contribuciones y lista de participantes; el tercer volumen contendrá les restantes documentos de experiencias.

Las opiniones expresadas en los documentos y en los informes son las de los autores y participantes y no necesariamente las de la Organización de Las Naciones Unidas para la Agricultura y la Alimentación.

Este volumen ha sido preparado bajo la Sección de Datos Biológicos de la Dirección de Recursos Pesqueros y Explotación con la colaboración de: Dr. E. Clarke, Mr. S. Olsen.

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SOME APPLICATIONS OF OBSERVATIONS AND EXPERIMENTS ON FISH BEHAVIOR IN DESIGNING FISHING GEAR AND DEVISING TACTICS, WITH SUGGESTIONS FOR FUTURE STUDIES

by

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Abstract

A brief review of some of the more recent literature on observations and experiments on fish behavior in relation to fishing gear and tactics is given. Some suggestions are made for considering fishing tactics as a problem in systems analysis. A conceptual scheme for a generalized fishery is presented.

QUELQUES APPLICATIONS AU DESSIN DES ENGINS DE PECHE ET A L'ELABORATION DES TACTIQUES DE PECHE D'OBSERVATIONS ET D'EXPERIENCES SUR LE COMPORTEMENT DU POISSON, AVEC DES SUGGESTIONS TOUCHANT LES ETUDES FUTURES

Résumé

La communication examine brièvement certaines des toutes dernières publications traitant d'observations et d'expériences sur le comportement du poisson en fonction des engins et des tactiques de pêche. Il est suggéré de considerer les tactiques de pêche comme un problème d'analyse des systèmes. L'auteur expose le modèle symbolique d'un système "pêche".

R/1

APLICACIONES DE OBSERVACIONES Y EXPERIMENTOS SOBRE EL COMPORTAMIENTO DE LOS PECES AL DISEÑAR ARTES Y FORMULAR TECNICAS DE PESCA CON INDICACIONES PARA ESTUDIOS FUTUROS

Extracto

Se hace un breve resumen de parte de la literatura más reciente sobre observaciones y experimentos acerca del comportamiento de los peces en relación con los artes y técnicas pesqueras. Se hacen indicaciones para considerar las técnicas pesqueras como un problema en los análisis de los sistemas. Se indica un esquema conceptual para una pesquería generalizada.

1 INTRODUCTION

The purpose of this paper is to review some of the more recent literature on: a) reaction of fish to a single non-biological stimulus, and b) reaction to multiple non-biological stimuli; both with a view toward suggesting applications of these observations in the design of fishing gear and the development of fishing tactics. Some tentative suggestions for an alternative approach to the general problem of applying behavioral and other information toward improved fishing tactics are also presented. The more specific problem of fishing gear design is considered as a sub-set of the general problem involving tactics.

The importance of non-biological stimuli and the behavioral responses of fishes generated by them is apparent to anyone faced with design, evaluation or improvement of fishing gear. However, the apparent diversity of non-biological stimuli, or fish species, life history stages, of fishing gear as well as the very nature of behavioral observations have precluded any formal method of quantifying these interrelationships with a view toward application. To date a number of ingenious direct and indirect methods in both the field and laboratory have been utilized to study fish behavior under defined conditions. These methods include: observations and photographs by divers, rafts, submarines, underwater television, echo sounding, comparative fishing experiments and tank studies. These methods have been recently summarized by Blaxter and Parrish (1966), who provide an excellent bibliography.

For the purposes of this paper it is acknowledged at the outset that the partitioning of non-biological stimuli into single and multiple categories is arbitrary. Indeed, this separation for purposes of description may have disadvantages from the point of view of increased understanding of complex phenomena. In addition, the exclusive consideration of non-biological stimuli is artificial and obviously includes interactions with biological factors. However, the reviewer's knowledge of the literature (albeit incomplete) pertaining to various aspects of fish behavior in relation to fishing gear and tactics suggests that there may be no more effective way of summarizing this material for the present.

It is suggested that both the quality and quantity of fish behavioral observations are adequate, but that the systematic application of this information to fishing gear and tactics is woefully inadequate. A possible reason for this may lie in the approach taken by the fishery scientist toward his problem. Almost without exception workers in the field of fish behavior have applied the so-called scientific method to their studies.

That is, the scientist is firstly an observer. Indeed, the scientist concerned with fish behavior has been a good one, evidenced by many published observations which are a result of carefully planned and executed experiments utilizing principles of sound experimental design (see, for example, Bagenal, 1958). Secondly, the scientist tries to describe in generality what he has observed as well as what might be expected in the future. Thirdly, he may make predictions based on his theories or observations which he carefully checks against facts repeatedly. This is very briefly the nature of the widely accepted scientific method which has been applied successfully to empirical sciences. It is suggested that the scientific method should not be an exclusive approach to the understanding of fish behavior in relation to fishing gear and tactics for reasons stated below.

If we consider a systematic application of behavioral or other information to fishing tactics with a view toward prediction it appears that we are concerned with a complex of man, machines, organisms and environment, a system, in which various inputs or outputs can initiate events removed in both time and space. Thus, in the application of information, behavioral or otherwise, toward a defined goal (prediction) we are dealing with a problem in systems analysis and not with science as defined above. The objectives of systems analysis are to analyze specific situations in order to ascertain how adequately these situations (systems) meet certain specific problems. These objectives are somewhat at variance with empirical sciences, which as mentioned above, attempt to describe or derive general laws. Systems analysis deals with the specific or unique situation. Its interest in a general description or observation is confined only to those occasions where a general truth permits a deduction toward the specific. Since the objectives of systems analysis and science differ, the methods of systems analysis and science differ. Some general suggestions for an approach toward the analysis of fishing activities, including behavioral observation, as a complex man-machine system will be made after briefly reviewing the recent results of observations on single and multiple non-biological stimuli with some applications. These observations, among others, are considered as necessary elements of a system, but they must then be utilized in the construction and analysis of a representative network of the system for useful prediction.

2 SINGLE NON-BIOLOGICAL MECHANISMS

Blaxter and Parris (1966) have recently described the effects of moving netting on cod, haddock and herring. Their tank observations suggest a herding effect by "warps" and other parts of the gear by daylight with conspicuous devices producing the more profound effects. These effects are reduced at night, and the stimulus is believed to be visual.

Some possible suggestions regarding these and other studies of fish behavior to moving netting in the design of fishing gear and tactics include:

a) Herding devices (warps) aimed at increasing effective fishing width are probably relatively ineffective at night, in extremely deep water or in highly turbid water.

b) Increased tow speed in reducing net avoidance in the vicinity of a trawl mouth seems to be better than increasing the spread of the net. Saila and Flowers (this conference) also suggest an optimum theoretical ratio of towed net speed to average fish speed in order to maximise the probability of capture.

c) There seem to be reasonable opportunities for designing gear in order to exploit responses to visual stimuli under some well defined conditions for certain species. This applies to both fixed and moving gear and seems to merit further study.

d) Large mesh in the wings of trawls appears to be an advantage in reducing drag without necessarily lowering the catch (Cassie, 1955).

Woodhead (1966) has comprehensively reviewed the literature regarding fish behavior ir relation to light in the sea. Some possible applications of these observations of fish behavior in relation to light are suggested. A few observations and suggestions follow:

a) An understanding of threshold light intensities for herring drift net fishing (Blaxter and Parrish, 1965) can be utilised to minimise net avoidance at certai seasons, Blaxter (1964) has also demonstrated the spectral sensitivity of the herring eye and this information may provide a guide to future applications.

b) Although considerable work has been done on light attraction of fishes, its successful application is limited to a relatively few species under well defined environmental and physiological conditions. The conclusion of Kuroki, Nakayama and Ueno (1964) indicating the necessity for more tests to investigate effects of interacting factors on light attraction is fairly typical of our state of knowledge at present.

In spite of the appeal of Carruthers (1964), relatively little systematic work on the intensity and direction of sea-bed currents and their relation to fish and/or gear behavior seems to have been done as yet. Jones (1963) has postulated some interesting relations between nets and currents, but this remains to be adequately tested.

Temperature (its vertical distribution and short as well as long-term variations) is another non-biological stimulus with obvious biological implications. Hunter and Wisby (1964) suggest a temperature effect on the vertical direction of escape from a series of laboratory experiments. Field studies have also been carried out in respect to temperature and McKenzie (1964) indicates that the horizontal distributional limits of four tuna species are temperature limited. Hela and Laevastu (1961) have provided a general review of the influence of temperature on fish behavior and there is no question but that a well defined relation between some aspects of breeding biology and temperature exists for many marine species. More recently a relationship between monthly and annual surface temperature and hooking-rate variations in yellowfin tuna has been shown by Nakagome (1964). Nakagome (1965) has also indicated a relationship between the swimming depth of yellowfin and big-eyed tuna and seasonal temperature variations. Koto and Maeda (1965) have studied the movement of ground fish shoals and bottom temperatures in the Eastern Bering Sea. Again a relationship is postulated between water temperature and the abundance as well as distribution of certain bottom species.

In summarizing temperature effects, it is abundantly clear that temperature plays a dominant role in the distribution of marine fishes, and it significantly affects fishing tactics and even gear design. This general conclusion is not very different from that reached by Hubbs (1948) in an early review article on temperature effects. It appears that although we now have many more observations obtained more precisely the present attempt at a generalization is no stronger than that made some time ago.

Numerous experiments have been reported on electrical fishing as well as the behavior of fish in an electric field. These are covered in detail elsewhere in this conference. An example of a fairly recent study is that of McRae and French (1965) which describes the results of applying an electrical field as an adjunct to an otter trawl of conventional design. Some of these results appear to hold much promise - but again for specific situations which are limited.

3 MULTIPLE NON-BIOLOGICAL MECHANISMS

As mentioned previously, it is extremely difficult to partition non-biological stimuli into single and multiple categories. However, a specific example of the application of multiple stimuli to fishing methodology is given by Nikonorov and Pateev (1963) wherein both light and electricity are utilized in pump fishing for saury in the Caspian Sea. A general exposition and some methodology for evaluating interrelationships of the ocean environment and the productivity of marine organisms are given by Rudnev and Palii (1964). Some elements of a systematic approach to understanding and predicting hydrographic phenomena in relation to fisheries are suggested in the above paper. Okonski and Konkol (1961) have more specifically considered the daily migration of herring shoals and their reaction to fishing gear under diurnal light variations. Kawakami (1963) has reported on the movement of mackerel shoals related to diverse environmental factors with a view toward application in fisheries.

In general it appears that, with minor exceptions, the conventional approach used to study multiple non-biological stimuli has met with the same shortcomings as the study of single non-biological stimuli. In both cases the information obtained is valuable but its utility in prediction is questionable. It is suggested that a systems approach is desirable as a next step to consider simultaneously not only the biological properties of the populations of fishes and their behavioral responses to various stimuli, but also the complex of environmental, social economic and equipment variables which affect the outcome and ultimate success of a fishery. Even beyond this, the judgement of this experienced fisherman (or possibly a command and control center) must be effectively integrated with the techniques of systems analysis. The integration of judgment with specialized systems analysis poses unique problems of organization, for both personalities and techniques themselves. Few people involved with fisheries problems would argue that there is an effective substitute for experience or for judgments that can be made by experienced fishermen. At the same time analytical tools, such as systems analysis, can be developed and refined for marine fisheries. Decisions on fishing operations can be based on both experience and systems analysis. Bayes' formula for decision making may provide one method for the skilled fisherman to combine his own judgment with the results of systems analysis.

4 CONCEPTUAL SCHEME

The application of experimental design and modelling techniques are proposed as a plan for optimising the exploitation efficiency and the yield from a fishery. The model is conceived as a symbolic scheme exhibiting the interralatedness as closely as possible of the function of the total system and enabling continually improved prediction of the output response characteristics of the system for given input configurations. The model must be operational in the experimental sense and is not construed as a strictly mathematical scheme, or an ensemble of a priori concepts to be arbitrarily imposed on system operations. A preliminary plan of the proposed system is shown in Fig. 1 as a series of symbols depicting postulated man-machine combinations and interactions, all combining to produce a desired objective. The purpose of the experimental design is to assist in defining objectives, testing the system to measure objectives, and to determine contributions of various systems blocks to the objectives.

The objectives of an experimental design include means for measuring improvement of the proposed system over existing or past fishery exploitation methods. By improvement is meant (a) rational distribution of fishing effort to maximise the sustained catch and income from desired species per unit of effort, and (b) improved prediction ability for determining the concentration and composition of catchable stocks in the area under consideration. Criteria of improvement in both of the above cases could be quantified by measuring certain outputs, such as catch per unit investment spent on effort, and index values might be assigned to detection and identification probabilities. Obviously, the absolute magnitude of improvement would vary seasonally with reference to a particular geographic area and species. However, it does not seem prohibitively difficult to obtain indications of the efficiency of the integrated system at all times. Comparisons of the system with available catch, effort and monetary return data from previous years would be used for establishing a base and making continued evaluations.

Briefly, the model suggested is considered to be a symbolic representation of a system - in this case the environment, the organisms, man and the equipment he employs for surveillance and capture. The concept of a model is predicated on the assumption that it is possible to abstract from a complex system, certain pertinent and discernible relationships and to mathematize and quantify these relationships with a view toward describing the behavior of the system under all conditions. Initial steps of modelling consist of deriving concepts that describe the purpose, factors operating and pertinent parameters or state variables, all of which go toward erecting a frame of reference in which the model is to be operational. This phase is the one in which planned experiments are involved to define the above. Obviously, this has not yet been done in the scheme suggested nor systematically in any existing fishery. However, this work is entirely possible with existing equipment given adequate funds and time. When these are available the model could establish a theoretical experimental situation within which the entire system could be evaluated with respect to the previously defined criteria of effectiveness.

The preliminary flow chart, Fig. 2, gives some indication by means of a block diagram of a first approximation toward the distinctive logical and sequential steps in system modelling. It is submitted that test data from carefully planned experiments could provide the necessary quantitative empirical data to fill out the model and to evaluate it. Some of these are already available for certain fisheries. The model would then be continually improved and modified with new test data but would be regularly utilized to describe and predict the response of the system to the various inputs which are time variable.

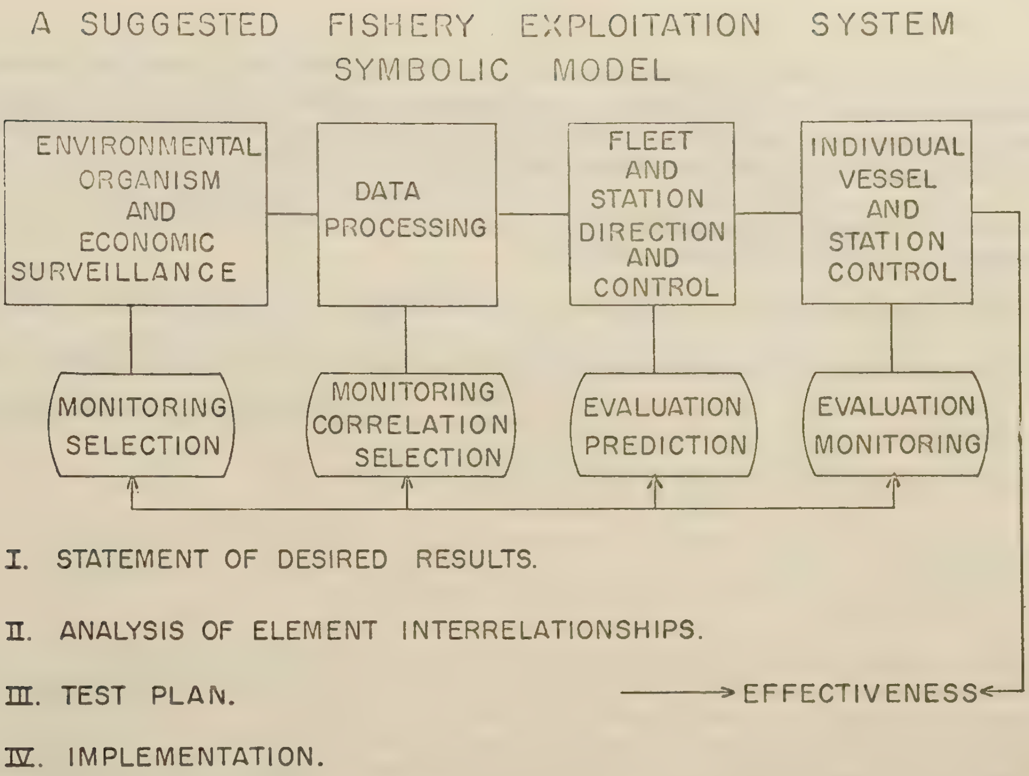
A SUGGESTED FISHERY EXPLOITATION SYSTEM
SYMBOLIC MODEL
ENVIRONMENTAL ORGANISM AND ECONOMIC SURVEILLANCE
DATA PROCESSING
FLEET AND STATION DIRECTION AND CONTROL
INDIVIDUAL VESSEL AND STATION CONTROL
MONITORING SELECTION
MONITORING CORRELATION SELECTION
EVALUATION PREDICTION
EVALUATION MONITORING
I. STATEMENT OF DESIRED RESULTS.
II. ANALYSIS OF ELEMENT INTERRELATIONSHIPS.
III. TEST PLAN.
IV. IMPLEMENTATION.
EFFECTIVENESS

Fig. 1 A suggested fishery exploitation system symbolic model

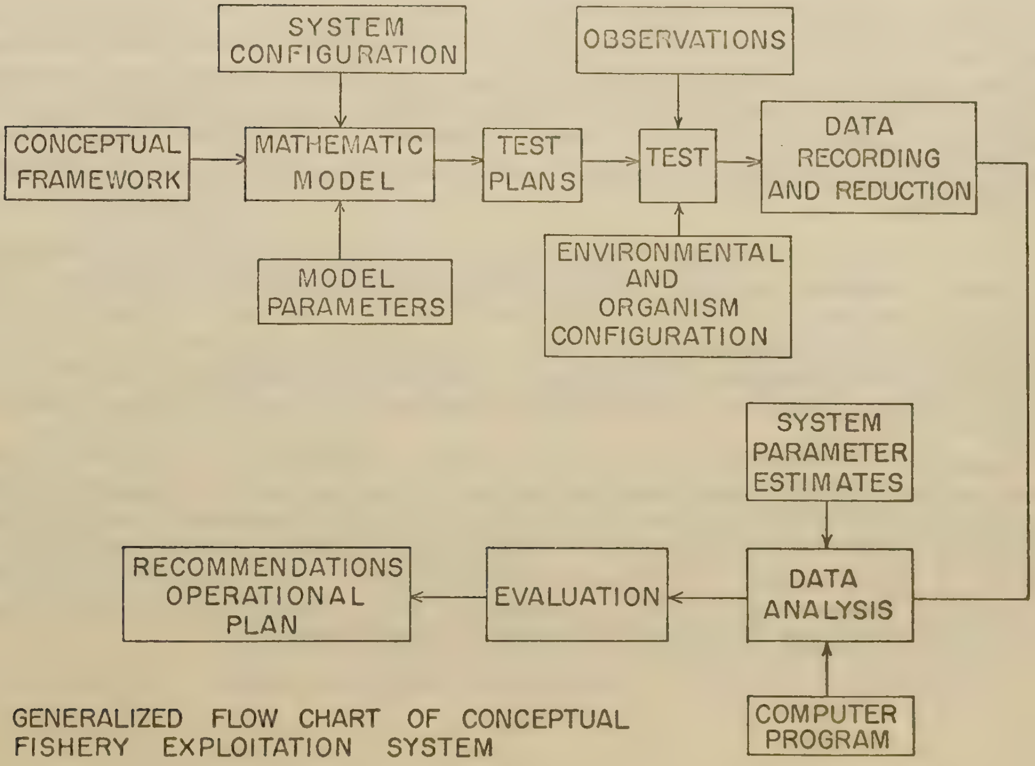
SYSTEM CONFIGURATION
OBSERVATIONS
CONCEPTUAL FRAMEWORK
MATHEMATIC MODEL
TEST PLANS
TEST
DATA RECORDING AND REDUCTION
MODEL PARAMETERS
ENVIRONMENTAL AND ORGANISM CONFIGURATION
SYSTEM PARAMETER ESTIMATES
RECOMMENDATIONS OPERATIONAL PLAN
EVALUATION
DATA ANALYSIS
COMPUTER PROGRAM
GENERALIZED FLOW CHART OF CONCEPTUAL FISHERY EXPLOITATION SYSTEM

Fig. 2 Generalized flow chart of conceptual fishery exploitation system

The conceptual approach suggested above for the analysis of a complex system, such as marine fishery, involves certain steps. The approach is based on assuming the existence of systems and that these systems can be conceived to consist of elements and element-pair relations. The analysis of any complex system seems to involve:

a) Preliminary selection and classification of the system elements affecting the predesignated problem

b) Initial determination of the existence of direct relations between element pairs

c) Restatement of system elements and direct relations to achieve greater consistency

d) Mathematical modelling of those elements and relations which lend themselves to it

e) Model evaluation in terms of completeness or adequacy

f) Description of relations not represented by the mathematical models

g) Judgment integration of the model and description

It should be appreciated that any conceptual representation of a system, since it is not the system itself, can represent only some of the system's attributes and interrelationships. For this representation to be meaningful, it must structure all those attributes and interrelationships which are relevant to the purpose for which the system is analysed. In addition, the representation must be fairly easy to manipulate. Finally, the judgment of the fisheries manager or operator must be integrated with the techniques of systems analysis. The integration of judgment with results of systems analysis is believed to embody the concepts of a priori, a posteriori and conditional probability.

5 DISCUSSION

Although the survey of literature is admittedly incomplete, it seems clear from it that the research on fish behavior in relation to gear and tactics has not been permissive of effective generalizations in terms of application. An alternative approach to improved fishing tactics (including prediction) including behavioral observations with systems analysis has been suggested in a very general framework. This latter scheme involved proceeding from a broad conceptual framework to a specific objective or objectives for a particular fishery.

The promise of such an approach seems technically and perhaps soon, economically feasible as well. However, details such as particular oceanographic equipment configurations for data gathering, the electronic and data handling components that go into data acquisition, interrogation sequences and computer configurations are still rapidly developing, and it would seem unreasonable to specify this more precisely at present. These elements, among others, must be structured for the specific problem and its objectives.

In a recent book on systems analysis Watt (1966) has outlined the general nature of systems analysis in ecology which provides the basis for rational management of marine populations. In the same book Paulik and Greenough (1966) have presented some mathematical tools for use in designing better salmon fishery management systems. The authors also discussed a specific model of a net fishery for salmon which embodies biological, economic and social interrelationships. This latter model, if conceived for a specific situation, would be a working example of the kind of system suggested in this paper.

It remains to be seen how soon the new generation of highly instrumented satellites and arrays of moored or free-floating buoys will be providing the necessary data for the environmental elements of a proposed system. It certainly seems appropriate at this time however, to consider carefully the conceptual scheme or system which can utilize this information for reliable prediction and control of a particular fishery.

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A REVIEW OF FIELD OBSERVATIONS ON TUNA BEHAVIOR

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Abstract

Observations of tuna behavior are reviewed for feeding, schooling, sounding in relation to the thermocline, associations with other organisms and objects, swimming speeds, attraction to surface disturbances, and repulsion by sound and light. Most of the observations were made in the pole-and-line, trolling, longline, and purse seine fisheries for tuna.

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ETUDE DES OBSERVATIONS FAITES SUR LES LIEUX CONCERNANT LE COMPRTEMENT DU THON

Résumé

Des observations sur le comportement du thon sont étudiées sous les aspects suivants: alimentation, rassemblement en bancs, sondage des animaux en fonction de la thermocline, associations avec d'autres organismes ou objets, vitesses de nage, attraction causée par les perturbations en surface, et réaction de fuite déterminée par le bruit ou la lumière. La plupart des observations ont été rassemblées dans les pêcheries de thons à la canne et à l'hameçon, à la traîne, à la palangre, et à la senne tournante.

EXAMEN DE LAS OBSERVACIONES SOBRE EL COMPORTAMIENTO DE LOS ATUNES

Extracto

Se reseñan las observaciones hechas sobre el comportamiento de los atunes durante su alimentación, agrupamiento y la sumersión con respecto a la termoclina, asociaciones con otros organismos y objetos, velocidades de natación, atracción por perturbaciones en la superficie, y repulsión por el sonido y la luz. Casi todas las observaciones se hicieron durante la pesca de atún con caña, con curricán, con palangre y con red de cerco de jareta.

1 INTRODUCTION

Tunas are schooling fishes of the tropical and temperate seas of the world. Most are pelagic, although some species are found only near land. Generally, they are captured on lines or in nets. Line fishing includes pole-and-line fishing with live bait, trolling, and longlining. Net fishing includes purse seining, trap fishing, and gill-net fishing (Brock, 1959; Takayama, 1963).

Field observations on the behaviour of tunas have mostly been made during pole-and-line fishing, trolling, longlining and purse seining. Since the first three methods require that the fish be hungry, many of the observations from line fishing concern feeding behavior. Purse seining does not depend on hunger of the fish, but rather on the availability of schools near the surface of the sea. The few observations on the relation between the structure and depth of the thermocline and success of capture have been made in the purse seine fishery. Observations on schooling and associations with other organisms and objects have been made in connection with all methods of capturing tunas. Some field observations have been made from structures or vehicles especially constructed for viewing underwater activity.

2 FEEDING BEHAVIOR

Schooling of tunas is disrupted when the fish are actively feeding. The success of the pole-and-line fishery depends on this activity, which has been described as a "feeding frenzy" (Strasburg and Yuen, 1958). When in such a state tunas indiscriminately take any small object in the water and thus are vulnerable to pole-and-line fishing. On several occasions, I have examined stomach contents of skipjack tuna, Katsuwonus pelamis, immediately after capture and have found cigarette butts and pieces of paper and wood, all of which probably were washed from the deck of the ship or were thrown overboard during fishing. In the pole-and-line fishery of the eastern Pacific, fishermen, when they have run out of live bait, have been known to use uncooked macaroni and other materials to maintain skipjack tuna or yellowfin tuna, Thunnus albacares, in a feeding frenzy. In the waters of New Guinea, fishermen have chummed yellowfin tuna with chopped cabbage (Hiroshi Nakamura, personal communication).

Water sprays are used in the pole-and-line fisheries of Japan and Hawaii. Rippling of the surface by the sprays is believed to enhance the feeding frenzy (Strasburg and Yuen, 1958). Many of the fishermen in Hawaii believe that the sprays help hide the fishermen from the tuna by rippling the sea surface. Some believe that the rippling serves as a refuge for the bait, and others that the rippling tends to make the lures indistinguishable from the bait. Yuen (1962a) observed that water sprays increased the response of skipjack tuna when certain species of live bait were used, but not when others were used. He stated that the sprays may affect the behavior of the bait rather than stimulate the skipjack tuna directly.

Schooling may not be disrupted during feeding at night. Bullis and Juhl (1967) observed little tuna, Euthynnus alletteratus, in a feeding phalanx, in which the little tuna remained in a compact school while feeding. They observed this formation at night after baitfish had gathered closely around a light set in the water.

Strasburg and Yuen (1958) observed that the presence of blood or extract from tuna skin in the water and sounds produced by pounding on the hull of the ship appeared not to affect the biting rate of skipjack tuna.

The type of prey also appears to affect the biting rate of tuna. For example, Strasburg (1961) found that skipjack tuna in Hawaii that had been feeding on juvenile Holocentrus lacteoguttatus and postlarval Synodus variegatus tended to sound more frequently during pole-and-line fishing than skipjack tuna that had been feeding on other organisms. Yuen (1959) noted that skipjack tuna feeding on fast-swimming prey could be hooked at a faster rate and for a longer period than those feeding on slow-swimming prey. Yuen (1962a) also found that live bait was more effective than dead bait.

Biting rate of tuna in relation to fullness of stomach or stage of digestion has been studied by several authors. Uda (1933) and Tominaga (1957) reported that skipjack tuna with empty stomachs and those with full stomachs may bite either well or poorly. Fish between these two extremes tend to bite more poorly the less they have in their stomachs, according to Uda (1933). Suyehiro (1938) and Hotta (1960), however, found that skipjack tuna which bite well generally have empty stomachs. Yuen (1959) observed that the duration of response to chum was negatively correlated with stomach volumes and with the stage of digestion of the dominant contents of the stomach.

Skipjack tuna display vertical bars on their sides during feeding (Strasburg and Marr, 1961). Kishinouye (1923) and Tominaga (1957) stated that fishermen could expect good catches when skipjack tuna exhibited these bars.

Experiments with artificial baits were conducted at sea in Hawaii by Tester, Yuen, and Takata (1954). They tried to attract tuna to the stern of a vessel by leaving a trail of extracts of flesh and viscera of skipjack tuna, extracts of flesh of yellowfin tuna, and extracts of live bait. They also tried chumming with inedible objects such as strips of aluminium foil and pellets of calcium carbide which effervesced. They also chummed with edible objects such as gelatin capsules, pieces of macaroni, and strips of agar impregnated with concentrated extracts and aluminium powder. All of their trials were unsuccessful. Okabayashi (1964) tested minced bait made from shrimp, herring, sand lance, saury, and anchovy mixed with noodles in trolling for frigate mackerel, Auxis thazard, near Japan. The efficacy of these baits was in the order listed. None was as good as live anchovy.

Artificial bait has also been tested for catching tuna by longline. Imitation squid were made from latex sponge rubber containing micaceous powder to give it luster. They were soaked in squid oil to provide odor and taste. Catches with this artificial squid were only half those with the usual saury bait (Koyama, 1959).

Midwater trolling for yellowfin tuna and albacore, Thunnus alalunga, has been tried recently by Japanese longliners. Fishermen aboard the vessels had noticed that yellowfin tuna and albacore often rose to the surface to eat waste bait thrown overboard. Surface trolling for these tuna had not been particularly successful. The fishermen thought that visibility of the trolling gear at the surface was responsible for the poor catches. A Japanese manufacturer suggested that a diving board be used, so that trolling could be done in midwater. Use of this method has produced significant increases in catches. (Japanese Tuna Market Report no. 21, May 23-26, 1966; Tuna Research Foundation, Inc., Ferry Building, Terminal Island, California 90731, U.S.A.).

3 SCHOOLING BEHAVIOR

The number of tuna in a school can range from few to many. On 30 July, 1966, a research vessel from the Tropical Atlantic Biological Laboratory of the U.S. Bureau of Commercial Fisheries, Miami, Florida, was travelling near the Bahama Islands. Bluefin tuna, Thunnus thynnus, estimated to range from 22 to 68 kg were seen along the ship's course for 2 1/2 h. Bell (1963) reported that in August, 1958, a total of 3,600,000 kg of bluefin tuna was taken by 36 purse seiners from a single school off San Benito Island in the eastern Pacific. Idyll and de Sylva (1963) stated that blackfin tuna, Thunnus atlanticus, in the Gulf of Mexico, around Cuba, and in the Lesser Antilles have been seen, especially when the seas were calm, in schools so large that the sight "defied the imagination".

Almost all species of tuna have been reported in mixed schools of two or more species. (For references, see Species Synopses in Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species, FAO Fisheries Report no. 6, vol. 2, 1963). After observing mixed schools through an underwater viewing chamber and studying motion pictures of them, Yuen (1962b) concluded that such schools are distinct species-specific schools drawn together by a common stimulus, such as food. A favorable spawning area may also draw together schools of different species. Yoshida and Nakamura (1965) observed what appeared to be a single, large school that subsequently was found to be several small schools of frigate mackerels, Auxis thazard and Auxis rochei, congregated in an area that divided the windward from the leeward side of an island. Milt flowed from captured males; the ovaries in the females were spent.

Joseph and Barrett (1963) observed skipjack and yellowfin tunas in a baitwell. The erratic and excited behavior of skipjack tuna abated when the skipjack tuna were in the presence of yellowfin tuna, which exhibited a much more subdued behavior. Skipjack tuna thus may be more vulnerable to purse seines when they appear in schools mixed with yellowfin tuna.

Schools of tuna usually consist of fish of the same size. Even in mixed schools, the individuals tend to be about the same size, perhaps as a result of their swimming speeds (Brock, 1954; Sette, 1950). Small fish simply cannot keep up with large fish over an extended period.

In Australian waters, small schools of bluefin tuna have been reported as "wild" and difficult to chum, but large schools of many closely packed individuals ("ripplers") are easier to chum (Robins, 1963).

Tominaga (1957) has observed that schools of skipjack tuna which bite well maintain an orderly formation, an unvarying speed, and a uniform direction; they create small, uniformly spaced ripples on the surface of the sea, and expose no more than the tip of their dorsal fins; one or two fish at the head of the school may jump out of the water; the fish are not frightened by an approaching vessel. In contrast, poorly biting schools are those with a disorderly formation; direction of advance is not fixed; the school tends to break into smaller schools, and waves on the surface are large and unevenly spaced; fish leap near the middle or at the rear of the school; and fish sound and reappear repeatedly when approached by a vessel.

Some tunas and mackerels school at night, apparently either by the light from the moon or from biological luminescence. Schools of yellowfin and bluefin tunas and Pacific mackerel, Scomber japonicus, in the eastern Pacific and Atlantic mackerel, Scomber scombrus, in the western Atlantic (Sette, 1950) are caught at night by purse seines. The luminescence of planktonic organisms disturbed by the fish aids the fishermen in locating the schools.

H. Nakamura (personal communication) has suggested that the finlets of yellowfin tuna and bigeye tuna, Thunnus obesus, and the blue streaks on the posterodorsal surfaces of skipjack tuna possibly serve as visual fixation points for schooling in these species and also as possible species and sex recognition marks. He once saw a motion picture of young yellowfin tuna, and noticed that the glitter of the finlets was very prominent. He said that fluorodermin, a fluorescent hydrocarbon, has been found in the skin of a number of fishes (Hirao and Kikuchi, 1958), and that this material may account for the glitter of the finlets of yellowfin tuna and the fluorescent qualities of the blue streaks in skipjack tuna.

4 SOUNDING BEHAVIOR IN RELATION TO THE THERMOCLINE

Purse seining for tuna has been most successful when a shallow upper mixed layer of the sea has been underlain by a thermocline with a sharp temperature gradient (Green, 1967). This sharp gradient is widely believed to deter tuna from sounding. Green warned, however, that temperature alone may not be the deterrent. The vertical distribution of dissolved oxygen may be equally important. For example, he found that the water contained 4 to 6 ml of dissolved oxygen per liter in the mixed layer, but only 1 ml or less just below the thermocline. He noted also that water in the thermocline was frequently very turbid.

Murphy and Niska (1953) found that in the central Pacific, where the bottom of the purse seine did not reach the thermocline, tuna often sounded to escape the net. And tuna sometimes enter a thermocline - sharp or not. Hester (1961) observed a purse seiner making a set on a school of skipjack tuna in the eastern Pacific. The school was observed for 14 min after setting began. Suddenly it disappeared from view and reappeared outside the net. Data from a depth recorder attached to the bottom of the seine and from a bathythermogram showed that the school had indeed gone down into the thermocline to escape.

5 ASSOCIATIONS WITH OTHER ORGANISMS AND OBJECTS

The association of tuna with other organisms and with floating objects is well known. Fishermen use their knowledge of such associations to locate schools of tuna. Among the associated organisms are other fishes (including sharks), live and dead whales, porpoises, and birds (Calkins and Klawe, 1963; Imamura, 1949; Royce and Otsu, 1955; Schaefer, Broadhead and Orange, 1963; Uda and Tsukushi, 1934). In the eastern Pacific, fishermen often find tuna swimming below certain species of porpoises, but not under others. In the central Pacific, however, fishermen believe that porpoises scare the tuna away from the vessel.

Tuna often congregate beneath logs, driftwood, floating vessels, and even dead whales (Schaefer, Broadhead and Orange, 1963; Tominaga, 1957). Yabe and Mori (1950) stated that schools may wander as far as 16 km from floating objects and then return. They stated that Japanese fishermen sometimes stop and wait for a school to return to a log. If this pelagic homing does occur, it implies that these tuna have some sort of navigational system.

Explanations for the association between drifting objects and fishes have been reviewed by Magnuson (1963). Recently, Gooding and Magnuson (in press) have postulated that refuge from predators was the most likely explanation, whereas Hunter and Mitchell (1967) favored the explanation that drifting objects served as visual fixation points for schooling.

In the central Pacific, pole-and-line fishermen rely almost wholly on sighting bird flocks to locate tuna. They even rely on the behavior of the birds to determine certain characteristics of the school - its size, the species and size of the fish, feeding state, and depth. The number and spread of the birds is an indication of school size. If the birds dive and circle fast and erratically, the fish are small. Birds flying high, then low, diving to the surface, and then rising steeply suggest the presence of dolphin, Coryphaena hippurus. If the birds are seen diving into the water, the tuna have driven their prey to the surface and are feeding actively. If the birds scatter or sit on the sea surface, the fish have sounded (Royce and Otsu, 1955). Similar bird behavior has been observed in the skipjack tuna fishery in Japan (Imamura, 1949).

6 SWIMMING SPEEDS

Swimming speeds of tuna have been reported by several investigators. Kishinouye (1923), Barsukov (1960) and Kramer (1960) did not describe their methods of measurement. Watanabe (1942) timed fish as they travelled a marked distance alongside a vessel. Instruments to measure speed attached to rods and reels have been used by Lane (1941) and Walters and Fierstine (1964). Nishimura (1963) used sonar. Yuen (1966) measured speed of swimming by analysing motion pictures. Speeds of skipjack tuna, yellowfin tuna, bluefin tuna, and albacore were measured by these authors. The speeds ranged from 0.8 to 25 m per sec. Yuen (1966) attributed the differences in speed to the activity and the size of the fish.

7 ATTRACTION TO SURFACE DISTURBANCES

Surface disturbances are believed by some fishermen to attract tuna. Hawaiian pole-and-line fishermen often slap the water with the ends of their poles when tuna are suspected to be near, but are not at the stern of the vessel. Mather (1964) reported that a surface disturbance such as a wake of a boat attracts bluefin tuna off the New England coast. Mather wrote that a fisherman who had had difficulty harpooning bluefin tuna transferred to a small boat which was being towed behind a motorboat, and soon harpooned several bluefin tuna that rose in the motorboat's wake. No lures were being trolled at the time.

8 REPULSION BY SOUND AND LIGHT

In the purse seine fishery of the eastern Pacific, various methods are used to repel skipjack and yellowfin tunas from openings in the net. Small explosives, called cherry bombs, with delayed fuses are thrown into the openings to prevent fish from escaping before pursing is completed. Sounds produced by hammering on the side of the vessel are also used. A flashing underwater light, hung from a rubber-insulated cord in the space between purse lines, is used during purse seining at night (McNeely, 1961).

9 OBSERVATIONAL VEHICLES AND INSTRUMENTS

Field studies of tuna behaviour have been made by using vehicles especially constructed for observing underwater activity. For example, viewing chambers attached to or built into a research vessel (Strasburg and Yuen, 1960), a floating raft with a viewing chamber (Gooding, 1965), and a small two-man submarine (Strasburg, Jones and Iversen, in press) have been used in the central Pacific.

Many behavioral observations have also been made on captive tunas held in large tanks on shore (Magnuson, 1965; Magnuson and Prescott, 1966). For example, color changes, feeding behavior, swimming behavior, and courtship behavior have been observed (Magnuson, ms.; Magnuson and Prescott, 1966; Nakamura, 1962; Nakamura and Magnuson, 1965; Walters, 1966).

Various types of acoustic instruments that have been used to observe tuna will be described by other conferees.

Underwater television has been used to observe the behavior of several commercial fishes, but, so far as I know, not that of tunas. Use of this instrument could add appreciably to field observations on the behavior of tunas in both line and net fisheries.

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SWIMMING SPEEDS OF FISH

by

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Abstract

Apparatus for measuring swimming speeds of fish are described and their limitations discussed. Burst speeds, maintained for a few seconds, are listed and related to body length. Only salmonids, scombroids and some freshwater and a few marine species seem capable of burst speeds equivalent to 10 body lengths (B.L) per second or more. Endurance speeds, maintained for minutes, are also listed and, in general, lie between 2 and 3 B.L/s, though salmonids and clupeids can probably maintain 4 B.L/s or more. It may be that burst speeds, which are more a function of white muscle, are sacrificed in some species for improved endurance or stamina, a function of red muscle. While there are considerable temperature effects on endurance, burst speeds are much more independent of temperature.

The biochemical background to activity, endurance and fatigue is discussed, showing how quite short periods of activity may lead to long-lasting biochemical effects in the blood and muscles, very intense activity perhaps raising the concentration of metabolites to a lethal level.

The hydrodynamics of fish in relation to drag and swimming performance are mentioned with respect to the power available in fish muscle.

Swimming performance is briefly related to the possible situations fish may meet in reacting to moving fishing gear.

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VITESSES DE NAGE DES POISSONS

Résumé

La communication décrit les dispositifs servant à mesurer la vitesse de nage des poissons et examine leurs limitations. L'auteur énumère des vitesses limites, ne pouvant être soutenues que quelques secondes, et les rattache à la longueur du corps des poissons. Seuls les Salmonidés, les Scombridés, certains poissons d'eau douce et quelques espèces marines paraissent capables d'atteindre une vitesse de pointe équivalant à 10 longueurs de corps par seconde ("B.L."/s) ou davantage. L'auteur mentionne aussi les vitesses soutenues (plusieurs minutes), qui se situent généralement entre 2 et 3 "B.L."/s quoique Salmonidés et les Clupéidés puissent probablement nager de façon suivie à "B.L."/s ou davantage. Il est possible que la vitesse limite, qui dépend davantage des muscles blancs, soit chez certaines espèces sacrifiée au profit de l'endurance (résistance), qui ressortit aux muscles rouges. Si l'endurance se ressent dans une grande mesure des variations de la température, la vitesse limite en est beaucoup plus indépendante.

L'auteur examine le fondement biochimique de l'activité, de la résistance et de la fatigue, montrant comment des périodes d'activité extrêmement brèves peuvent amener dans le sang et dans les muscles des modifications biochimiques de longue durée, une activité très intense pouvant peut-être même pousser la concentration de métabolites à un niveau mortel.

Diverses caractéristiques hydrodynamiques (résistance à l'avancement, nage) sont traitées en relation avec l'énergie musculaire du poisson.

Enfin, l'auteur rapproche brièvement les vitesses de nage des diverses situations dans lesquelles peut se trouver le poisson lorsqu'il réagit au déplacement des engins de pêche.

VELOCIDADES NATATORIAS DE LOS PECES

Extracto

Se describen aparatos para medir las velocidades que alcanzan los peces al nadar y se examinan sus limitaciones. Se enumeran las velocidades máximas que se mantienen durante unos cuantos segundos, relacionándolas con la talla de los peces. Unicamente los salmónidos, escombridos y ciertos peces de agua dulce, y unas cuantas especies marinas, parecen ser capaces de lograr velocidades máximas equivalentes a 10 veces su talla corporal (T.C) por segundo o más. Se indican también las velocidades que pueden resistir durante algunos minutos, las cuales, en general, varían entre dos y tres T.C/s, aunque los salmónidos y clupeídeos probablemente pueden mantener velocidades correspondientes a cuatro T.C/s o más. Es posible que las velocidades máximas, que están en función del tejido muscular blanco, se sacrifiquen en ciertas especies en favor de una mayor resistencia o estamina, que es una función del tejido muscular rojo. La temperatura influye mucho en la resistencia, pero muy poco en las velocidades máximas que mantienen los peces durante unos momentos.

Se examinan los antecedentes bioquímicos en relación con la actividad, la resistencia y la fatiga, indicándose que los períodos muy breves de actividad pueden tener duraderas consecuencias bioquímicas en la sangre y en los músculos, y que una actividad muy intensa quizá lleve la concentración de matabolitos a un nivel letal.

Se menciona la hidrodinámica de los peces en relación con sus cualidades natatorias y con la resistencia al avance, en lo que se refiere a la potencia existente en los músculos de los peces.

Se relaciona sumariamente la actividad natatoria con las posibles situaciones que los peces puedan encontrar al reaccionar ante la presencia de los artes de pesca en movimiento.

1 INTRODUCTION

Lists of swimming speed measurements taken from the literature are given by Bainbridge (1958), Nursall (1962) and Radakov (1964). From these and an examination of the results of earlier work it is at once clear that the variety of techniques and experimental conditions used, and the different criteria applied for defining swimming speed, make it extremely difficult to compare the results of different authors. In some cases very high values suggest that the technique was not sufficiently objective, or that adequate attention was not paid to inaccuracies inherent in certain types of apparatus. On the other hand rather low values make it questionable whether the subjects were in good condition, or whether stimulation in the experiments was of a sufficient order.

It is intended to review the methods used for measuring swimming speed and mention their faults, to give values for burst and cruising speeds, to mention the biochemical and hydrodynamical background and, finally, to relate the results to fishing practice.

2 TECHNIQUES OF MEASUREMENT

A number of devices have been used to assess the swimming speed of fish, both in still water and in currents.

(a) Timing fish in open water or tanks against a reference background. This has been done with a stop watch by Magnan (1929), Blaxter (1962) and Ryland (1963) and is most applicable to small specimens, such as fish larvae, where the movement over a measureable period is not too great. Burst speeds have been measured by ciné-photography in tanks by Magnan (1929), Gray (1953, 1957) and in more open conditions by Magnuson and Prescott (1966) and Yuen (1966).

(b) Timing fish in channels or culverts. Timing the movement of fish in still water over fairly long distances was used by both Blaxter and Dickson (1959) and Ohlmer and Schwartzkopff (1959). More commonly, the time taken to swim a measured distance against a flow has been recorded, for example by Wales (1950), Blaxter and Dickson (1959), Ohlmer and Schwartzkopff (1959), Dow (1962) and Weaver (1963, 1965).

(c) Timing fish in tubes. A similar technique to (b) but where the flow is contained within a tube has been applied by many workers such as Blaxter and Dickson (1959), Bishai (1960), Ryland (1963), Brett (1964, 1965) and Beamish (1966a).

(d) By fish maintaining station relative to the background, either in a rotating annular tank, or in an annular tank containing still water with a screen rotating outside it ("pseudorheotropism"). The first of these techniques was developed by Regnard (1893) and brought to perfection by Bainbridge (1958, 1960) who combined it with a ciné-camera record. Less elaborate apparatus on a similar principle was used by Fry and Hart (1948), Radcliffe (1950), Paulik and DeLacy (1957), Paulik, Delacy and Stacy (1957), Brett *et al.*, (1958) and Boyar (1961). Jones (1963) adapted the second technique, used previously for measurements of spectral sensitivity, flicker-fusion and acuity, to establish threshold currents for an orientating response.

(e) By attaching threads to fish and measuring the speed they run out. Both Magnan (1929) and Ohlmer and Schwartzkopff (1959) used this on fish already caught. A more elegant application is the "piscatometer" (Gero, 1952;

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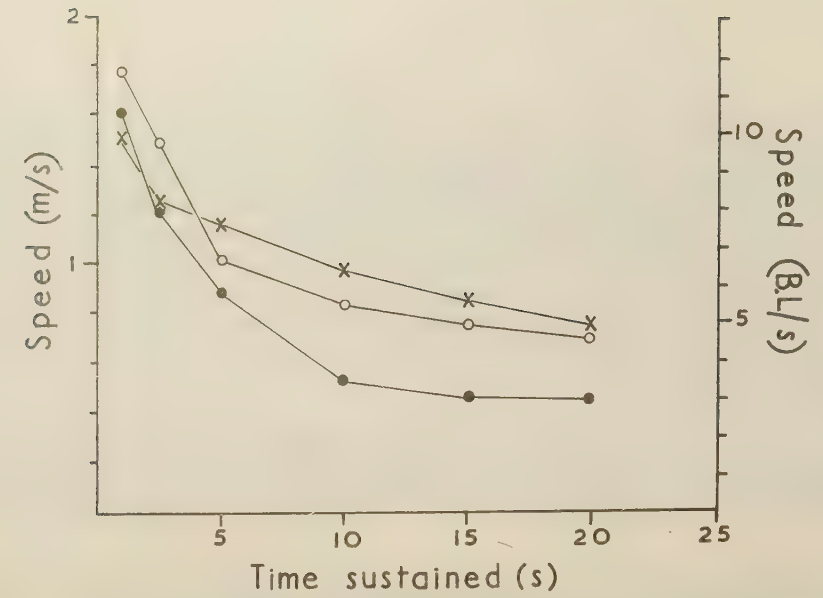

Fig. 1 Calculated relationship between speed and the time it can be sustained for three 15-cm fish; o dace, ● trout, x goldfish, (re-drawn from Bainbridge, 1960).

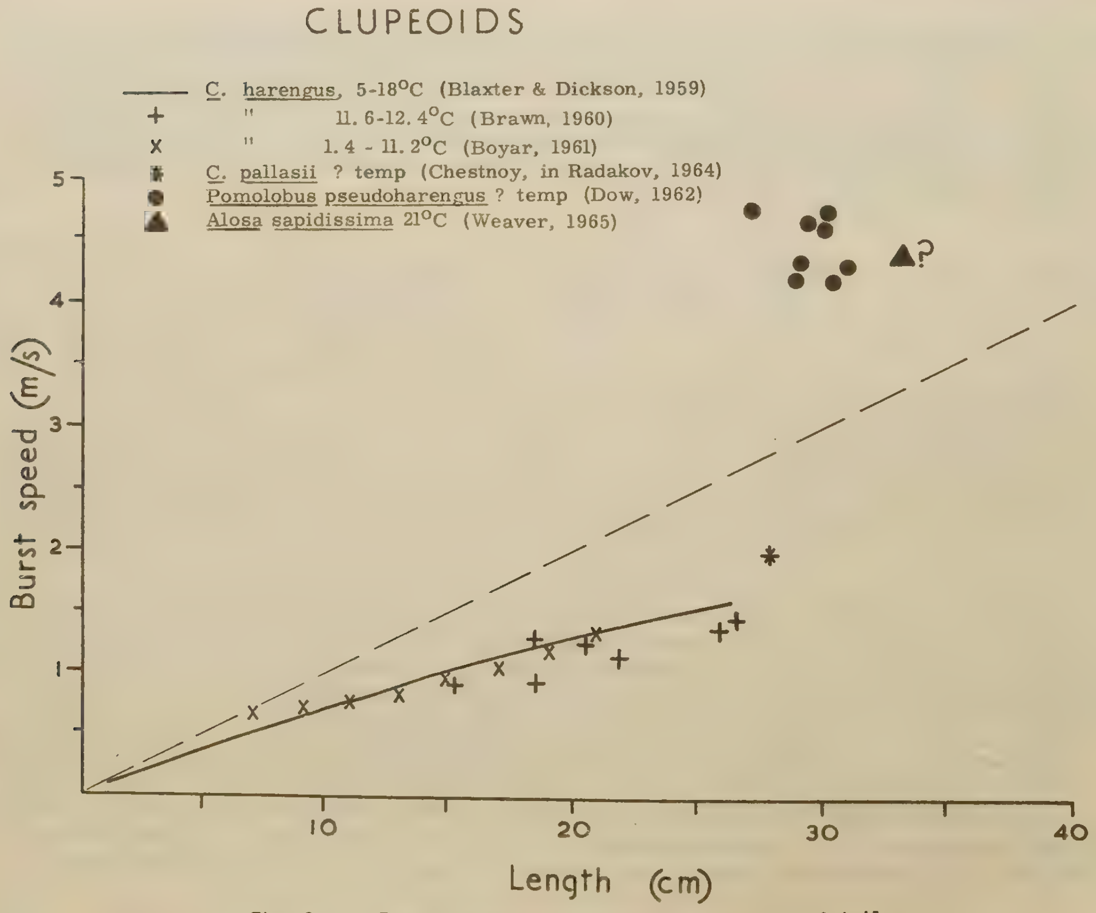

Fig. 2 Burst speeds of clupeoids; see key for details.

Walters and Fierstine, 1964) where wild fish are caught by line already attached to a revolution counter.

(f) Modifications and extensions of the above techniques, especially in open-water are found in the work of Brawn (1960) who observed, by television, herring in a towed underwater cage, and Aslanova (quoted by Radakov, 1964) and Blaxter and Dickson (1959) who towed troughs and tubes by motor boat to get substantial rates of flow in apparatus with a wide cross-section. Cushing and Jones (1966) watched fish under natural conditions by means of sector-scanning sonar, while Johnson (1960) tracked adult salmon by means of attached sonic transmitters.

(g) Other methods such as obtaining values of minimum speed by tag returns or by fishery statistics are not considered in this paper.

3 BURST SPEEDS AND ENDURANCE - A GENERAL CONSIDERATION

The multiplicity of methods, and of criteria, for assessing maximum speeds make it difficult to compare the results of different authors. The use of ciné-film permits a very accurate measurement of acceleration and velocity over fractions of a second. Bainbridge (1958) suggested the criterion that the speed should be maintained for one minute and from a study of the literature concluded that ten body lengths/second (B.L/s) could be maintained by good performers over this order of time. Some authors (e.g. Gero, 1952; Gray, 1953; Walters and Fierstine, 1964; Weaver 1963, 1965; Yuen 1966), were clearly measuring speeds over a much shorter time, as did Bainbridge himself. The criteria adopted by different authors depended largely on the accuracy of their measurements, ciné-cameras or piscatometers permitting the measurement of very short bursts. Blaxter and Dickson (1959) required their fish to swim at least ten body-lengths while Brawn (1960) and Boyar (1961) noted speeds which could be maintained for 1 min and 30 secs respectively. In relation to escape from trawls, where burst speeds of very short duration (1 sec or less) would seem less generally applicable, except for escape from peripheral regions of the trawls path, values of maximum speed are given in the following pages on the assumption that they can be maintained for the order of 1 to 5 secs. This may be related to Fig. 1 where data from Bainbridge (1960) are re-drawn to show how the speed drops rapidly when the duration of the burst increases from 1 to 10 secs. Clearly then many of the values which are to be given do not represent the absolute maximum of the fish.

Of especial interest is Regnard's (1893) conclusion, supported by Bainbridge (1958), that the maximum speed of fish is in the region of 10 B.L/s. This is also shown in Fig. 1, and in all subsequent figures giving burst speeds, to help in establishing further any general relationships between size of fish and their speed.

Endurance or cruising speeds have been standardised over different lengths of time, e.g. 20 to 25 min by Fry and Hart (1948), 60 min by Brett (1964, 1965) and varying lengths of time by Beamish (1966a). Stamina in a number of species was tested by chasing them, when fully extended, to exhaustion (Blaxter and Dickson, 1959). It is clear from Fig. 1 and from the work of Bainbridge (1960) and Brett (1964) that a cruising speed not far above that sustainable for very long periods may be established fairly quickly, perhaps within a minute or so. While it is again almost impossible to relate the results of different authors, from the trawling point of view a 60 min standard seems a desirable one, but it is probably true that beyond 1 to 5 min of swimming the reduction in speed required to swim for a longer time is not great. Brett's (1963) suggestion that cruising speed should be related to the biochemical changes within a fish, the maximum cruising speed obtaining when no oxygen debt is incurred, seems a good one and might well be applied in future work where biochemical tests are available.

For the present purpose, work to-date shows that 2 to 3 B.L/s can be maintained for long periods by most species and 3 to 4 B.L/s by salmonids. Though this may be modified by temperature, exercise and other factors, on graphs showing endurance a 3 B.L/s line is included for purposes of later discussion.

Before listing data from the literature another word of caution is necessary. Most of the techniques used have inherent sources of error, and only in some has account been taken of them. They are:

(a) Problems of water flow. In culverts and tubes there is rarely a rectilinear front or flat velocity profile; due to friction and other factors the flow is reduced near the walls. This is discussed by Ryland (1963) and has, in particular, been corrected by Brett (1964, 1965) who used especially designed inflows in his respirometer. The errors lie not only in overestimates of current flow near such surfaces but in the apparent ability of some fish to select regions of a culvert, flume or river where the velocity is minimal or where there are standing waves or areas of turbulence. This is mentioned especially by Fields et al (1954) and also by Ohlmer and Schwartzkopff (1959), Osborne (1961) and Weaver (1963). Conversely salmonids Weaver (1963) will sometimes select the flume with the higher velocity when given a choice, and it is well-known that salmonids require an exit flow to enter a fish ladder. Davidson (1949) found that the cruising speeds of eels and young salmon increased with the velocity of the current; it may well be a general principle that anadramous fish perform better in moving water.

(b) The condition of the fish may also affect their performance. Exercised coho salmon Oncorhynchus kisutch fatigued less quickly and showed a higher maximum sustained speed than unexercised fish (Brett et al., 1958). Captive stocks of brook trout, Salvelinus fontinalis had a poorer stamina than specimens of similar origin brought up in the wild (Vincent, 1960). Bainbridge (1962) using rainbow trout, Salmo irideus found that the best of the exercised fish were better performers than the best of the unexercised fish, though on average there was no difference.

Clearly fish which have exerted themselves (see section on biochemical effects) have also a reduced performance and this may well be of importance where fish are escaping from nets in a closely fished area of sea.

Maturing freshwater fish of many species (Aslanova, quoted by Radakov, 1964) showed a reduction in swimming performance as they became ripe. Mohr (1964) found a decrease in the excitability of herring during the spawning season as judged by the Netzsonde or headline echo sounder.

(c) Temperature has a considerable influence on cruising speeds (Fry and Hart, 1948; Brett et al., 1948; Beamish, 1966a), but according to a number of authors its effect on burst speeds is slight (Blaxter and Dickson, 1959; Brett, 1963, 1964; Beamish, 1966a). Though temperatures are given with the data which follow no attempt has been made to separate results obtained at different temperatures.

(d) Activity and swimming performance may vary with salinity in salmonids. Houston (1959) found that young chum salmon (Oncorhynchus keta) had a reduced locomotor performance in sea water, while Groves (1960) found that the duration of swimming of young sockeye salmon (O. nerka) increased in salt water.

(e) A final and worrying factor in swimming speed assessment is the possible reduction in performance of captive fish as a result of capture itself, confinement, lack of exercise, inadequate food and general stress. The slow dispersion of metabolic products is described in a later section on the biochemical background. This may account in part for some discrepancies between authors using wild and captive fish of the same or similar species. Little attempt has been made, except with salmonids, to establish any such differences. A hint of short, very rapid bursts in marine commercial species (not identified) is contained in a paper by Cushing and Jones (1966) who observed, by sector-scanning sonar, fish reaching to a midwater trawl; one specimen moved 8 m in 0.25 sec and a further 7 m in the next 0.25 sec. This is far in excess of speeds recorded under aquarium conditions for any of the species likely to have been present at the time (except tuna).

4 BURST SPEEDS AND ENDURANCE - VALUES OBTAINED

It is proposed to include under burst speeds those measured over a matter of a few seconds. With a few exceptions, which are mentioned, endurance speeds are applied to those measured over periods of a minute or more. Experimental temperatures are listed in the figures when they were available.

4.1 Clupeoids

(a) Clupea harengus (herring). This species has been more thoroughly investigated over a very wide length range than almost any other marine or freshwater (see Figs. 2 and 3). Larvae of 10 mm had burst speeds of about 5 cm/s rising to about 30 cm/s at a length of 20 mm, the development of the caudal fin at 15 to 18 mm having a substantial effect (Blaxter, 1962). Based on a criterion of swimming at least ten body lengthsthe speeds for larger herring ranged from 0.5 m/s at 7 cm to 1.5 m/s at 25 cm (Blaxter and Dickson, 1959). The values extracted from Boyar (1961) were based somewhat differently i.e. that 10 percent of the fish should maintain the speed for 30 sec and those of Brawn (1960) 50 percent for 1 min. The fairly general agreement between these authors suggests the herring, though not capable of high burst speeds, can nevertheless maintain a relatively high speed for a fairly long period; thus burst and endurance speed may not be as different as in some other species.

Observations by a headline echo sounder (Netzsonde) attached to a pelagic trawl (Schärfe, 1960) showed that shoals of adult herring could keep ahead of the trawl at a towing speed of three knots (1.5 m/s), while the best catches were obtained at towing speeds of 1.75 m/s or more. Chestnoy (quoted by Radakov, 1964) found speeds of 2 m/s for 28 cm Pacific herring (? by a similar technique). High and Lusz (1966), from observations by SCUBA divers on herring about 15 cm in length swimming within the mouth of a trawl, considered they could maintain 1.13 m/s (over 7 B.L/s) for 20 min or more. These endurance values, with those from Boyar (1961), are plotted in Fig. 4. Over 1 h his herring were able to maintain 2 - 3 B.L/s and considerably higher rates over shorter periods, e.g. 5 B.L/s for 10 min. Blaxter and Parrish (1966) found that adult herring in a large tank showed a marked change in response to model nets towed at speeds above 1.3 m/s suggesting that they were unable to maintain this speed (5 B.L/s) for more than a few seconds.

Jones (1962), from echo-sounding observations, deduced that herring (? adult) could maintain position in a tidal flow of 90 cm/s (c. 3 B.L/s) and in experimental work (1963) found that juvenile herring would swim at

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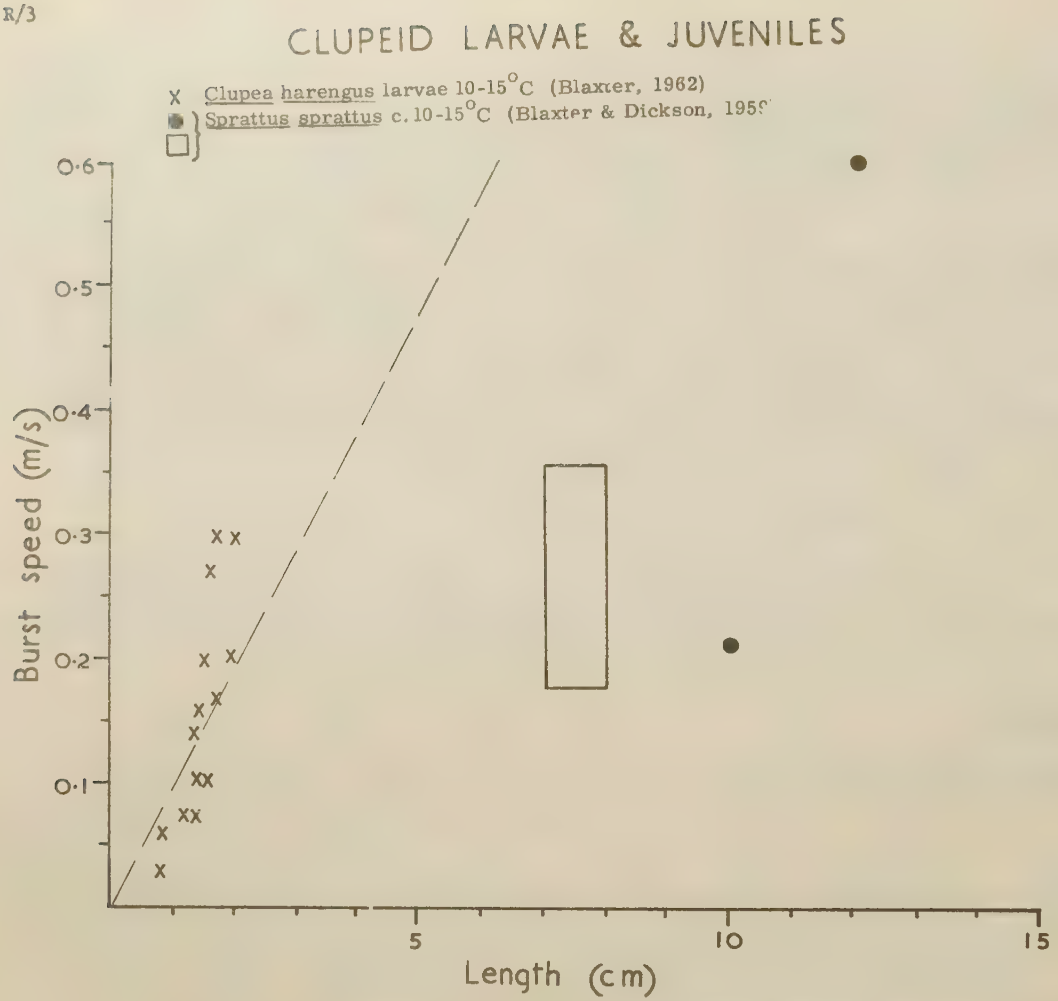

Fig. 3 Burst speeds of clupeid larvae and juveniles; see key for details.

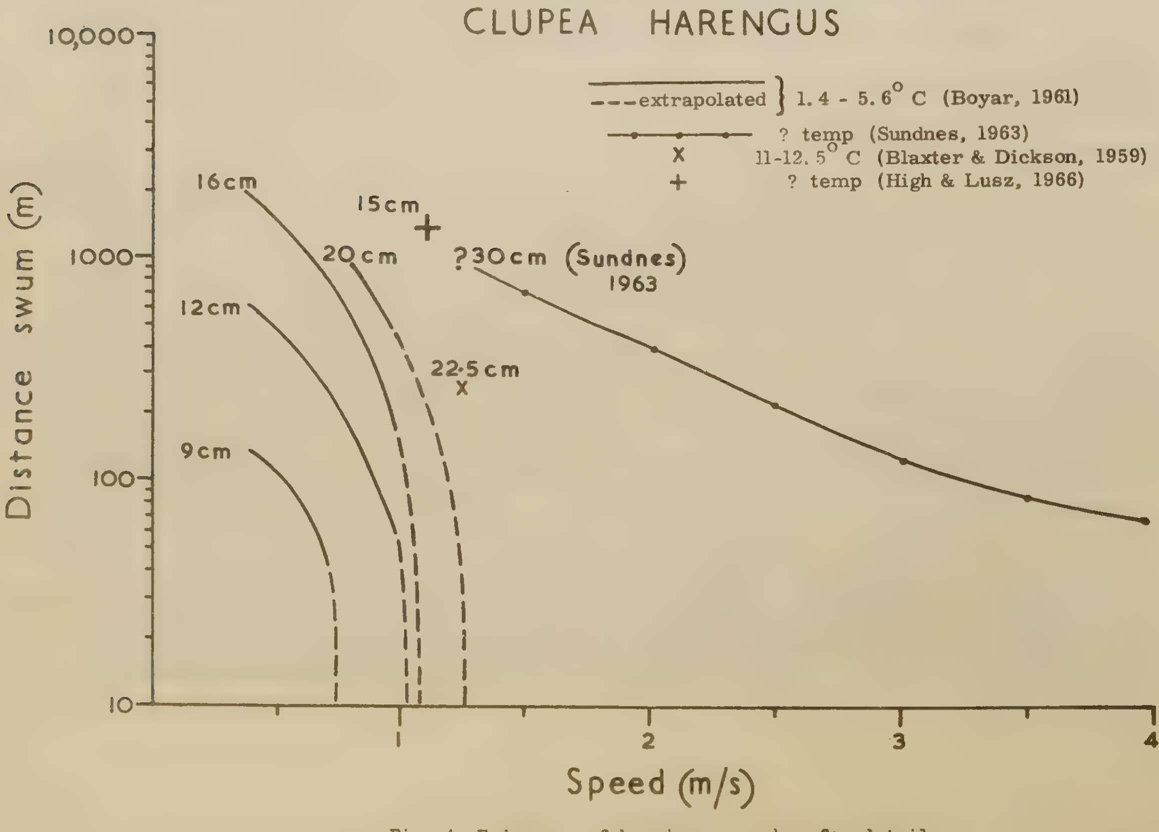

Fig. 4 Endurance of herring; see key for details.

3 to 4 B.L/s for long periods in response to a moving background of stripes. Hempel (personal communication) observed juvenile herring in an annular tank swimming at 4 to 5 B.L/s for hours at a time.

Though no marked temperature effect has been noted for cruising speeds of herring, there is good agreement between different authors that 3 to 4 B.L/s, or even slightly more, is valid as an estimate of swimming over a long period. Probably burst speeds of 6 to 8 B.L/s are applicable to herring, below the theoretical 10 B.L/s figure. The values of swimming calculate by Sundnes (1963) from drag and respiration measurements are less in accord. His suggestion that 700 m could be swum at 1.5 m/s (?5 B.L/s) or 50 m at 4 m/s (? over 13 B.L/s) is not supported by experiment.

The only available evidence of endurance speeds in herring larvae are figures from Bishai (1960) that larvae of 6.5 to 7.5 mm can maintain 0.58 to 1.03 cm/s for one hour, in the region of 1 B.L/s.

(b) Sprattus sprattus (sprat). Some juvenile sprat were tested by Blaxter and Dickson (1959), see Fig. 3, and their burst speeds found to be somewhat less than herring of similar size.

(c) Engraulis encrasicholus (anchovy). The only available data appear to be those of Lebedev (1936, quoted by Radakov, 1964) who gives 0.65 to 0.8 m/s for fish of unknown length swimming in an annular tank for a considerable time, while Radakov (1962) observed shoals of anchovy swimming, without any agitation, within a trawl towed at 0.75 m/s.

(d) Alosa sapidissima (shad). Weaver (1965) timed shad, length unstated, making headway in a flume through which water was passing at 3.5 to 4.2 m/s. Although it is not possible to calculate their precise speed from the data available, it would seem that they were exceeding these values if, in fact, they were traversing parts of the flume where the current was typical.

(e) Pomolobus pseudoharengus (river herring). Using a similar method Dow (1962) measured speeds of 4.15 to 4.85 m/s for fish of 27.1 to 31.2 cm (see Fig. 2), that is about 14 to 17 B.L/s. These high values may have been due to the use of natural conditions without the need to handle the fish. The fish may also have been stimulated by flow. Nevertheless, there is again a possibility of overestimating speed if they were selecting low velocity areas in the flume.

4.2 Gadids

Despite the commercial importance of this group they have been neglected in relation to their swimming abilities. Only Blaxter and Dickson (1959) measured burst speeds in four species, based on swimming at least ten body lengths, see Fig. 5. The values are low, mainly from 1 to 1.5 m/s, even for large fish. Cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) showed an inability to maintain speeds above 1.3 m/s when presented with model nets moving in a large tank (Blaxter and Parrish, 1966).

Some endurance values for gadids, see Fig. 6, are based mainly on the work of Beamish (1966a). A speed of around 3 B.L/s was maintained for 10 min by cod, depending on temperature. Over 1 h 2 to 3 B.L/s could be sustained. With the abundance of those species it should not be difficult to check the experimental results by observations underwater.

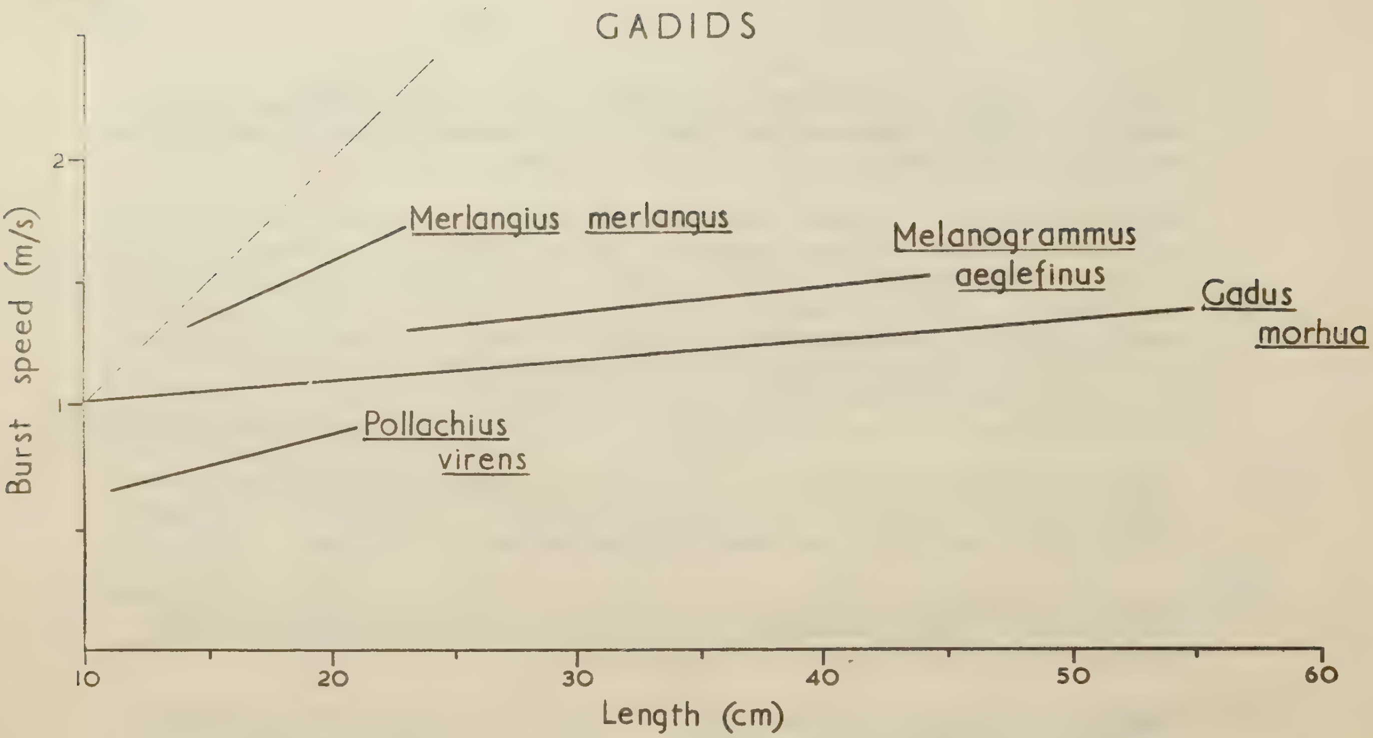

Fig. 5 Burst speeds of gadids at 9 to 17°C (from Blaxter and Dickson, 1959).

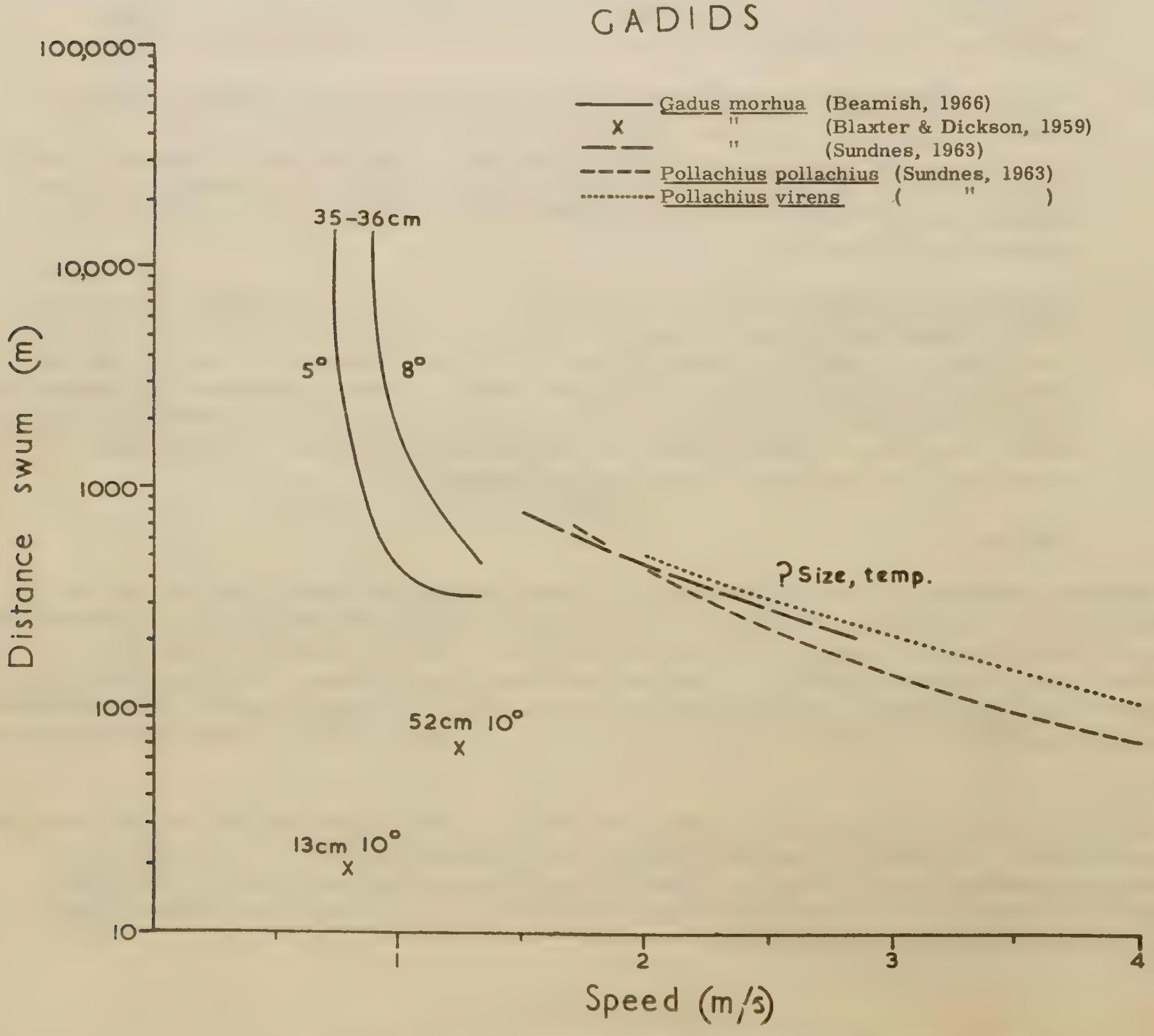

Fig. 6 Endurance of gadids; sizes and temperatures given on graph; see key for other details

Jones (1963), using three species of gadids viz. cod, whiting and whiting-pout *G. luscus*, found that they maintained 1 to 2 B.L/s when following a striped screen rotating round an annular tank for a period long enough to consider it within their cruising capabilities.

4.3 Pleuronectids

Estimates of burst speed for *Pleuronectes platessa* (plaice), *Platichthys flesus* (flounder), *Limanda limanda* (dab) and *Microstomus kitt* (lemon sole) by Blaxter and Dickson (1959) are shown in Fig. 7. For fish of commercial size speeds of the order of 1 to 1.25 m/s were found, well below the theoretical 10 B.L/s line. Only the darting speeds of larvae measured by Ryland (1963) were of this order.

Endurance values for *Pseudopleuronectes americanus* (winter flounder) from Beamish (1966a) are re-calculated in Fig. 8. They are equivalent to 4 to 5 B.L/s for 10 min, temperature having a rather mixed effect. His experiments did not extend beyond about 30 min so that a 60 min figure is not available. Again, the theoretical values from Sundnes (1963) assign the plaice a considerably better performance than would appear from experiments.

4.4 Scombroids

Data for *Scomber scombrus* (mackerel), *Thunnus albacares* (yellowfin tuna), *Euthynnus (Katsuwonus) pelamis* (skipjack tuna), *Thunnus thynnus* (bluefin tuna) *Sarda chiliensis* (bonito) and *Acanthocybium solandri* (wahoo) are given in Fig. 9. The specimens used were in general much bigger than the fish described so far and higher speeds approaching, and sometimes exceeding, 10 B.L/s were reported. Watanabe (1942) observed skipjack at 5 to 10 m/s as they swam alongside a research vessel. Yuen (1966) timed skipjack (up to 6.9 m/s or 14.4 B.L/s) and yellowfin (up to 5.4 m/s or about 10 B.L/s) by ciné-photography from an underwater viewing port in a research vessel. Magnuson and Prescott (1966) used a similar method for bonito in a tank, finding a maximum speed of 3.7 m/s (6.5 B.L/s) and cruising speeds, at 21 to 23°C, of 0.70 to 0.88 m/s (about 1.5 B.L/s). Walters and Fierstine (1964), with a piscatometer, measured speeds of 5 to 21 m/s (6 to 21 B.L/s) for yellowfin and 12 to 21 m/s (12 to 19 B.L/s) for wahoo. These high speeds were only maintained during very short bursts.

4.5 Salmonids

(a) *Salmo* species. Using *Salmo irideus* (rainbow trout) in a rotating, annular tank Bainbridge (1958, 1960) carried through a comprehensive study of various aspects of swimming, including burst speeds (see Fig. 1 and Fig. 10) by means of ciné-photography. Gray (1953) filmed the same species darting in a tank. Both authors found values of near to 10 B.L/s, as did Blaxter and Dickson (1959) working on *Salmo trutta* (sea trout and brown trout). Denil, quoted by Bainbridge (1958) gave measured or calculated speeds of 5.8 to 19.4 B.L/s for other salmonid species. Steelhead trout (*S. gairdneri*) from 61 to 82 cm were timed moving in different velocities of water in a flume by Weaver (1963), maximum speeds of 4.3 to 8.3 m/s (7 to 13 B.L/s) being calculated.

The endurance of rainbow trout has been examined by Bainbridge (1960, 1962). Speed drops greatly with the length of a burst (see Fig. 1). Above periods of 10 to 20 s the speed seems to decrease to about 3 to 4 B.L/s, which can probably be maintained near this level for long periods. Davidson (1949) found with fry of *Salmo salar* that 4 B.L/s could be maintained for

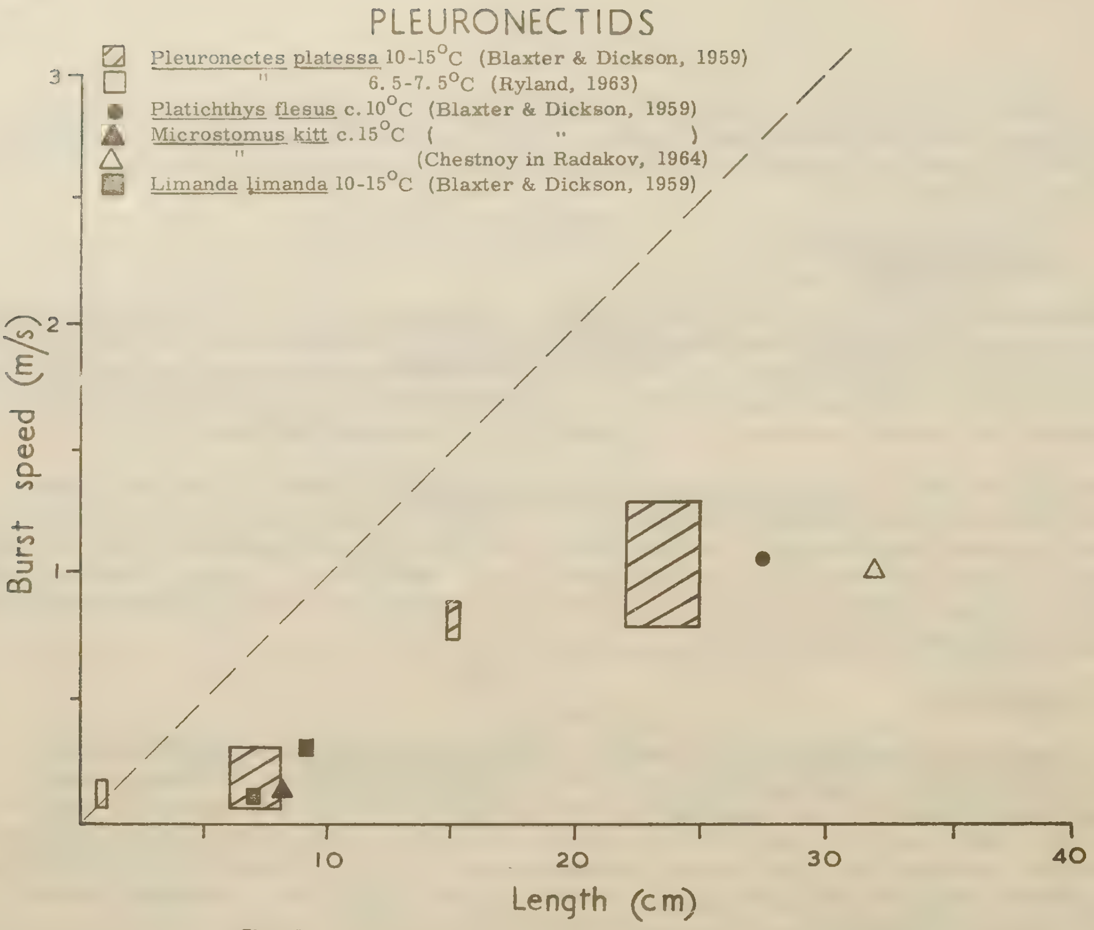

Fig. 7 Burst speeds of pleuronectids; see key for details.

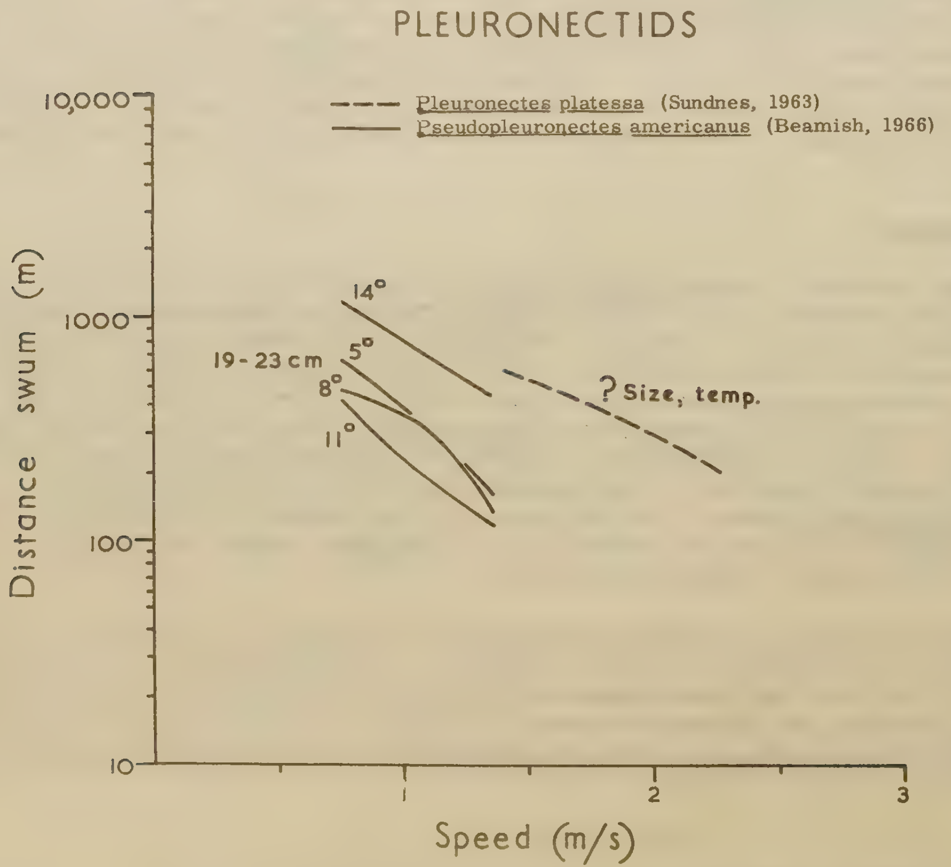

Fig. 8 Endurance of pleuronectids; temperatures given on graph.

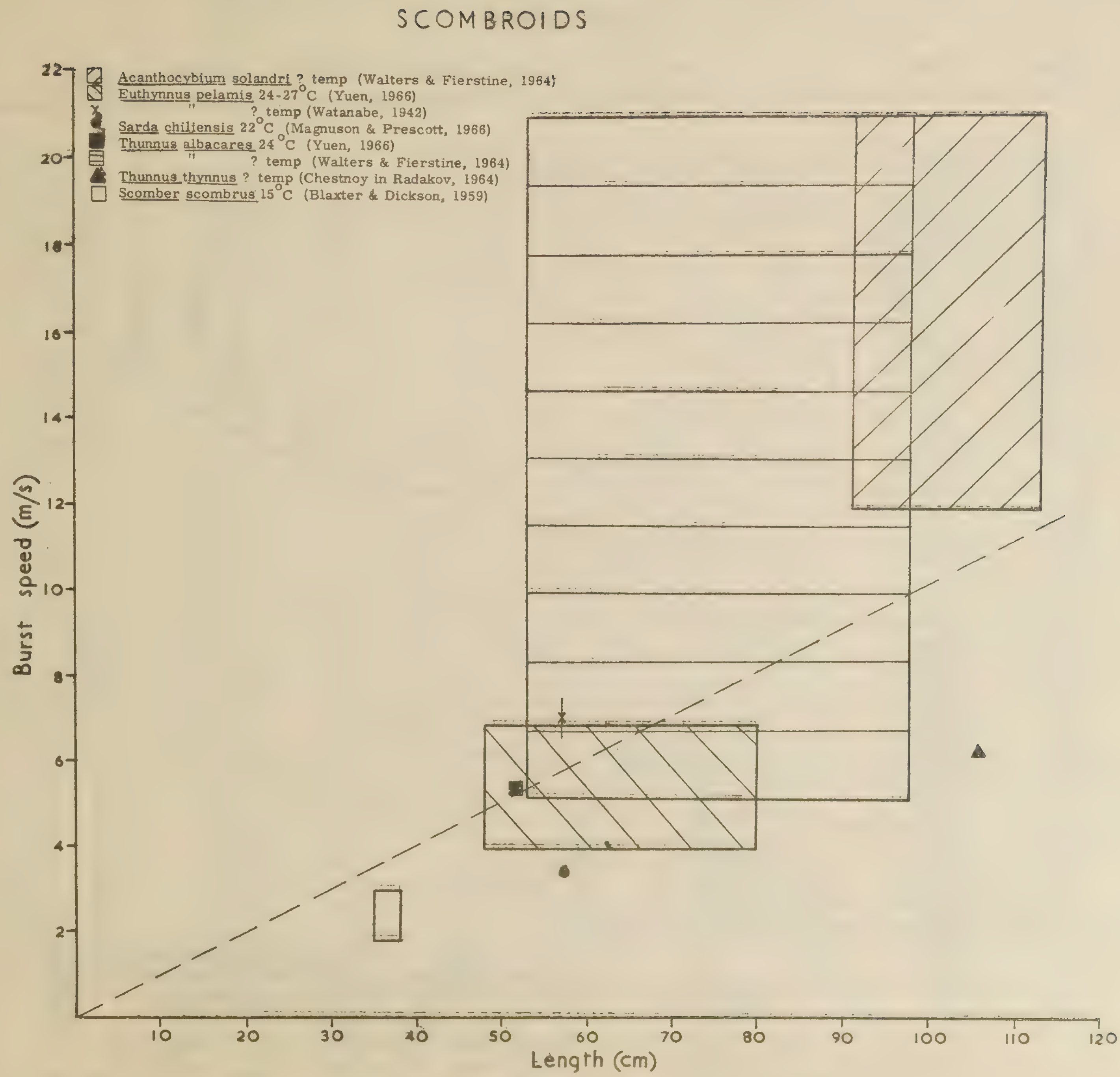

Fig. 9 Burst speeds of scombroids; see key for details.

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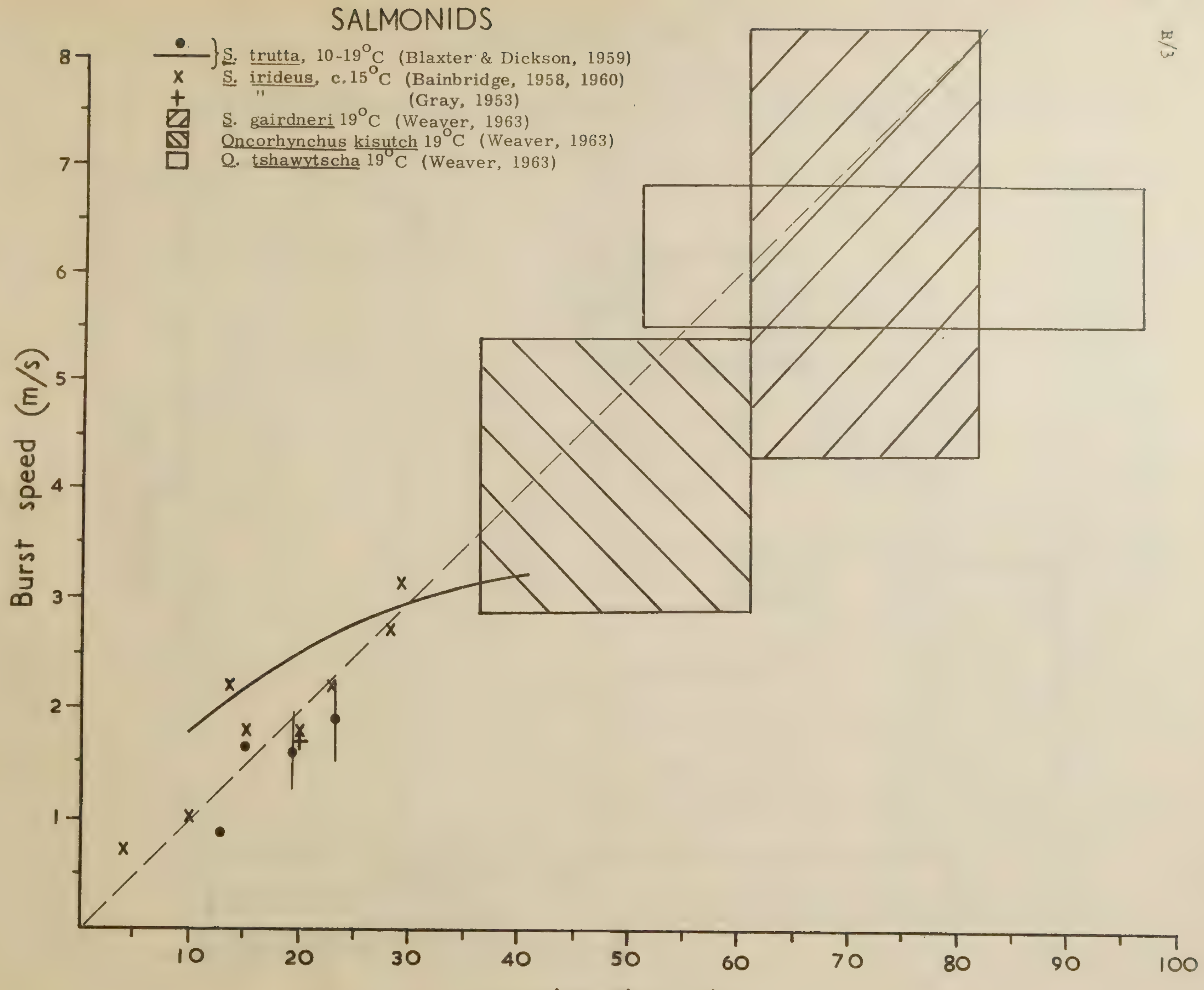

Fig.10 Burst speeds of salmonids; see key for details.

a considerable time, with a tendency for more rapidly-flowing water to increase the cruising speed. Paulik and DeLacy (1957) retained steelhead trout of average length 64 cm in a rotating tank and found they could cruise at 3.3 B.L/s.

(b) Oncorhynchus species. Weaver (1963), using different current velocities in a flume found coho (silver) salmon, O. kisutch from 36 to 61 cm with burst speeds from 3.0 to 5.4 m/s (6 to 9 B.L/s) and chinook salmon O. tshawytscha from 51 to 97 cm long with speeds from 5.5 to 6.8 m/s (from about 7 to 11 B.L/s), see Fig. 10.

Young coho salmon were placed in a flume with a current of about 1.2 m/s, (Fingers et al., 1954). Those of length 10.8 cm were all swept through within 5 min, and larger ones 21.7 cm in length all within 12 min. The endurance of young coho and sockeye (blueback) salmon (O. nerka) was assessed at different temperatures by Brett, Hollands and Alderdice (1958) in an annular, rotating tank. The highest cruising speed maintained for 1 h for sockeye, 35 cm/s (5.1 B.L/s), was at an acclimation and test temperature of 15°C and for coho at 20°C, 30 to 41 cm/s (4.7 to 5.6 B.L/s), depending on size. Temperature outside the optimum caused reduction in cruising speed to as much as 50 percent of the highest value. In later work, Brett (1964, 1965) extended these experiments to a wide age-range of sockeye salmon at a number of acclimation temperatures, using a specially designed "respirometer" tube, the water passing through it having a flat velocity profile. Using 18 cm fish he again found that cruising speeds maintained for 1 h were highest at 15°C (4.1 B.L/s), being 3.3 B.L/s at 5°C, 3.7 B.L/s at 10°C, 3.9 B.L/s at 20°C and 3.8 B.L/s at 24°C. Using a fixed acclimation temperature at 15°C he measured the cruising speeds maintained for 1 h by sockeye salmon from 7.7 to 53.9 cm. These ranged from 51.5 cm/s (6.7 B.L/s) to 143 cm/s (2.7 B.L/s), see Fig. 11.

Paulik and DeLacy (1957) tested sockeye (O. nerka) and coho (silver) (O. kisutch) salmon in a rotating annular tank, finding cruising speeds over long periods of 3.0 B.L/s for sockeye averaging 51 cm, and 3.4 B.L/s for silver salmon averaging 56 cm, in length.

Johnson (1960), by means of tags equipped with a sonic transmitter, found that chinook salmon swam at an average daytime speed of 0.6 m/s, with a net-up stream movement of 0.54 m/s. Burst of "short duration " against the current equivalent to 1.58 to 1.80 m/s were recorded.

4.6 Cyprinids and percids

(a) Carassius auratus (goldfish). Being a popular laboratory species the goldfish has been extensively studied. Results for measurements of burst speeds obtained from Bainbridge (1960) and Blaxter and Dickson (1959) are plotted in Fig. 12. There is good conformity with the line showing a speed of 10 B.L/s, which confirms the goldfish as a good laboratory subject.

Endurance studies are mainly due to Fry and Hart (1948), who used an annular, rotating tank and a wide range of test and acclimation temperatures. For each acclimation temperature there was an optimum temperature giving maximum cruising speed over 20 to 25 min. This optimum did not necessarily correspond with the acclimation temperature. In general the best performance, around 50 cm/s (estimated by Bainbridge (1960) as 6.4 B.L/s), was between 20 and 30° C. Radcliffe (1950) clipped various

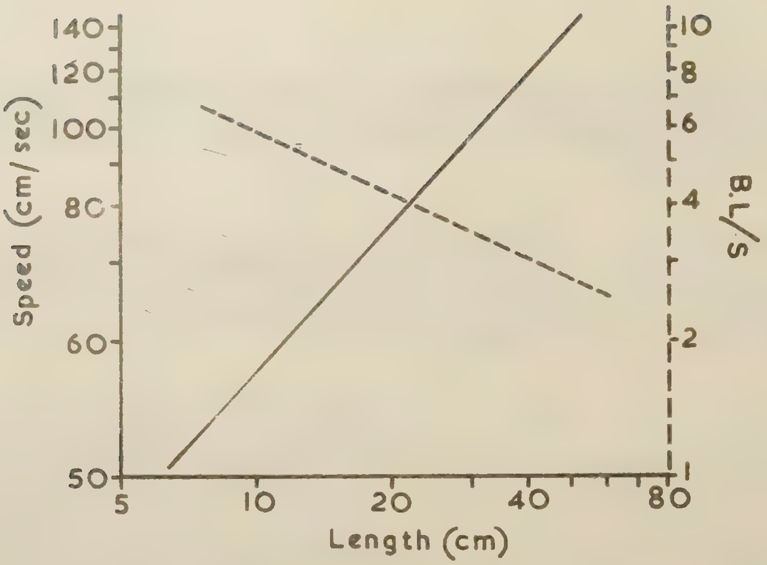

Fig. 11 Endurance speeds of sockeye salmon (maintained for 60 min) in relation to length at 15°C (re-drawn from Brett, 1965)

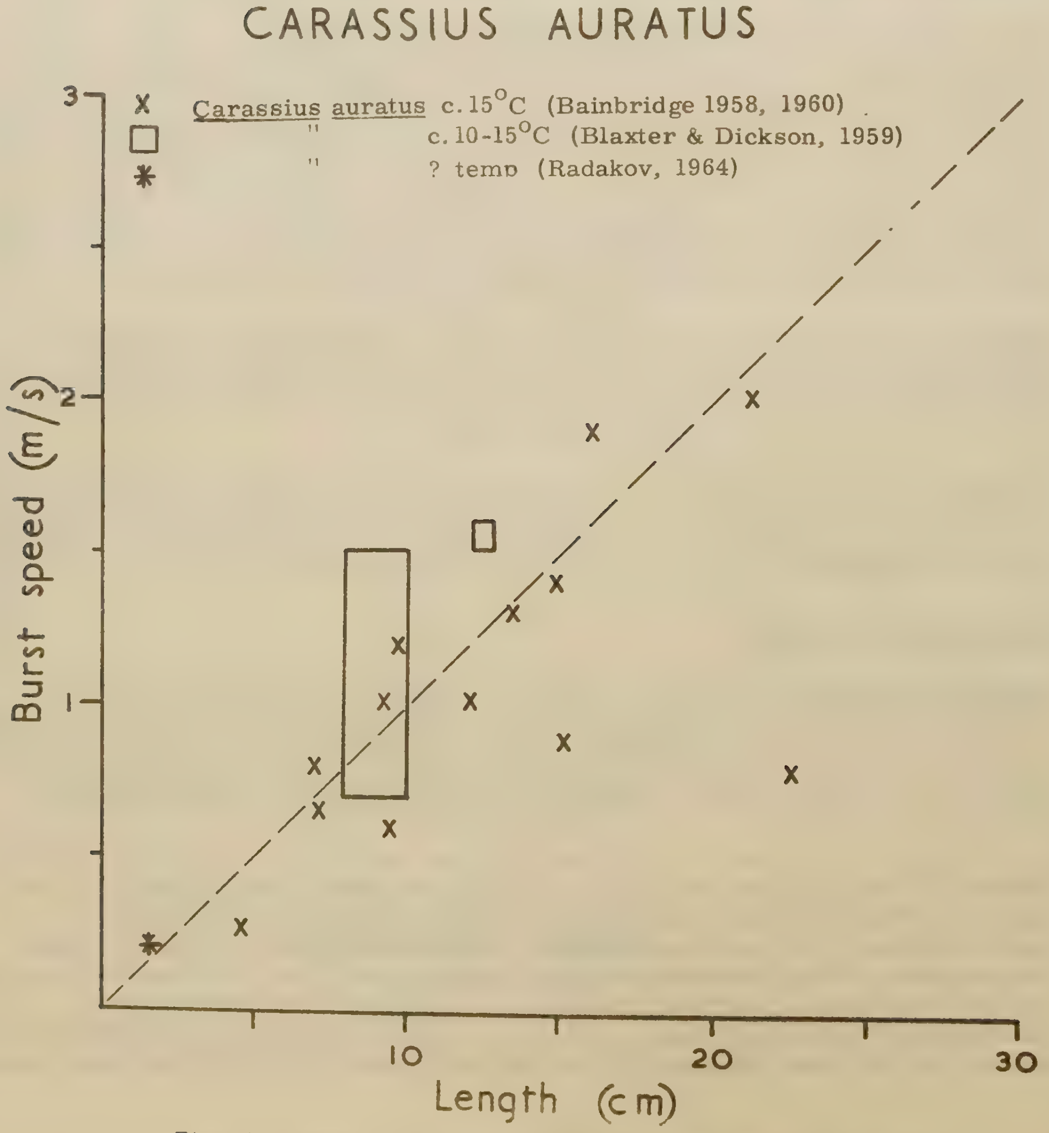

Fig. 12 Burst speeds of goldfish; see key for details

fins in goldfish and found, if anything, it slightly improved their cruising speed.

(b) Other species. Other cyprinids and percids which include Leuciscus leuciscus (dace), Rutilus rutilus (roach), Cyprinus carpio (carp), Abramis brama (bream), Scardinius erythrophthalmus (rudd), Perca fluviatilis (perch), Lucioperca sandra (pike-perch) and Esox lucius (pike) have been worked on by Gray (1953), Bainbridge (1960) and Ohlmer and Schwartzkopff (1959). The burst speeds for these are plotted in Fig. 13, showing in dace, carp and pike a good performance around 10 B.L/s. In other species the burst speeds did not exceed about 5 B.L/s.

The endurance speeds over 1 min for a number of species obtained by Aslanova (quoted by Radakov, 1964) using a "towed trough" are given in Fig. 14. The pecked line indicates 3 B.L/s showing that roach had a rather better performance than this, while bream, carp and pike-perch only managed 1.5 to 2 B.L/s.

4.7 Miscellaneous species

Burst speeds for a number of other species are given in Table I. In no case do they exceed 10 B.L/s. Other very high speeds have been reported in the literature. For instance Walford (1937) gave 30 m/s for the sailfish Istiophorus caught on a hook. Barsukov (1960) gave 25 m/s for tuna, 36 m/s for marlin and swordfish and 22 to 25 m/s for flying fish at take-off. Because the size of the fish and the means of measurement are not given, or possibly are not reliable, it was considered better not to accept such values, though they are extensively quoted in the later literature.

Endurance values over 1 min obtained by Aslanova (quoted by Radakov, 1964) are also shown in Fig. 14. Mullet (Mugil and Mullus) and horse mackeral Trachurus were able to maintain about 4 B.L/s over this period. Other endurance values were measured by Beamish (1966a) in redfish (Sebastes marinus), longhorn sculpin Myoxocephalus octodecimspinosus, sea raven Hemitripterus americanus and ocean pout Macrozoarces americanus. Redfish maintained 3 to 4 B.L/s for 10 min and probably 3 or rather less than 3 B.L/s for 1 h. The other species were not tested for so long and would appear to have had an endurance speed of about 2 B.L/s for 10 min.

5 BURST SPEEDS AND ENDURANCE - CONCLUSIONS

While 10 B.L/s or more may well be quite regularly attained in a number of groups, especially salmonids and scombroids, the swimming performance of many trawl-caught species, from the evidence available, suggests that they are rather poorer performers. Within the developing techniques of underwater observation it should not be long before more measurements are available in the natural habitat. For the present one might consider burst speeds of from 6 to 8 B.L/s more valid for such species.

Clearly, no hard-and-fast rule can be made relating speed to size of fish, in view of the great variety of body form. However, within a species various attempts have been made to calculate such a relationship. Bainbridge related speed (V) in cm/s to length (L) in cm and tail beat frequency (f) in beats/s, viz:

$$V = \frac{1}{4}\left\{ L\,(3f - 4)\right\}$$

for rainbow trout, dace and goldfish.

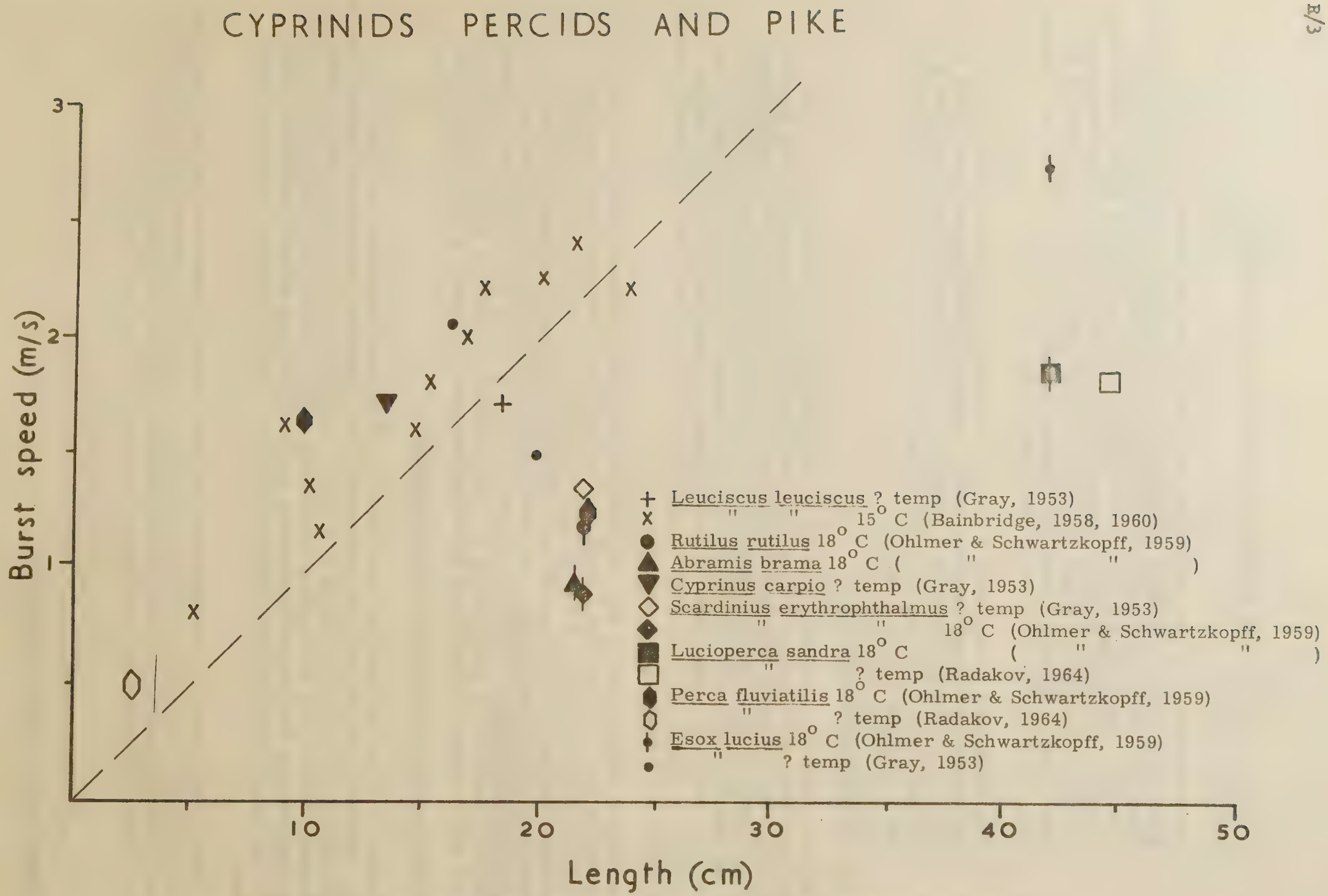

Fig.13 Burst speeds of cyprinids, percids and pike; see key for details.

Table I

Observations of burst speeds

Species	ave. length cm	Burst speed m/s	Burst speed B.L/s	Temp °C	Method	Author
Elasmobranchs (sharks)						
Carcharhinus leucas	153	5.3	3.4	?	Piscatometer	Gero (1952)
"	?104	4.1	3.9	?	"	"
Negaprion brevirostris	184	2.5	1.3	?	"	"
Teleosts						
Anguilla vulgaris (eel)	60	1.1	1.9	<10 ->15	Tube	Blaxter and Dickson (1959)
Blicca bjorkna (white bream)	2.2	0.3	15	?	Towed trough	Radakov (1964)
Catastomus occidentalis (sucker)	33	3.3	9.8		Flume	Wales (1950)
Gasterosteus spinachia (stickleback)	10	0.7	7.2	<10	Tube	Blaxter and Dickson (1959)
Gobius minutes (goby)	6.5	0.3	4.2	>15	Tube	"
Pholis gunnelus (butterfish)	10	0.3	3.0	>15	Tube	"
Promicrops itaiara (grouper)	?97	1.8	1.8	?	Piscatometer	Gero (1952)
Sphryaena barracuda (barracuda)	122-130	12.3	9,4 10.0	?	Piscatometer	"
Trigla sp. (gurnard)	18	1.3	7.4	10 ->15	Tube trough	Blaxter and Dickson (1959)
Zoarces viviparus (blenny)	6.4	0.2	3.1	<10 ->15	Tube	"

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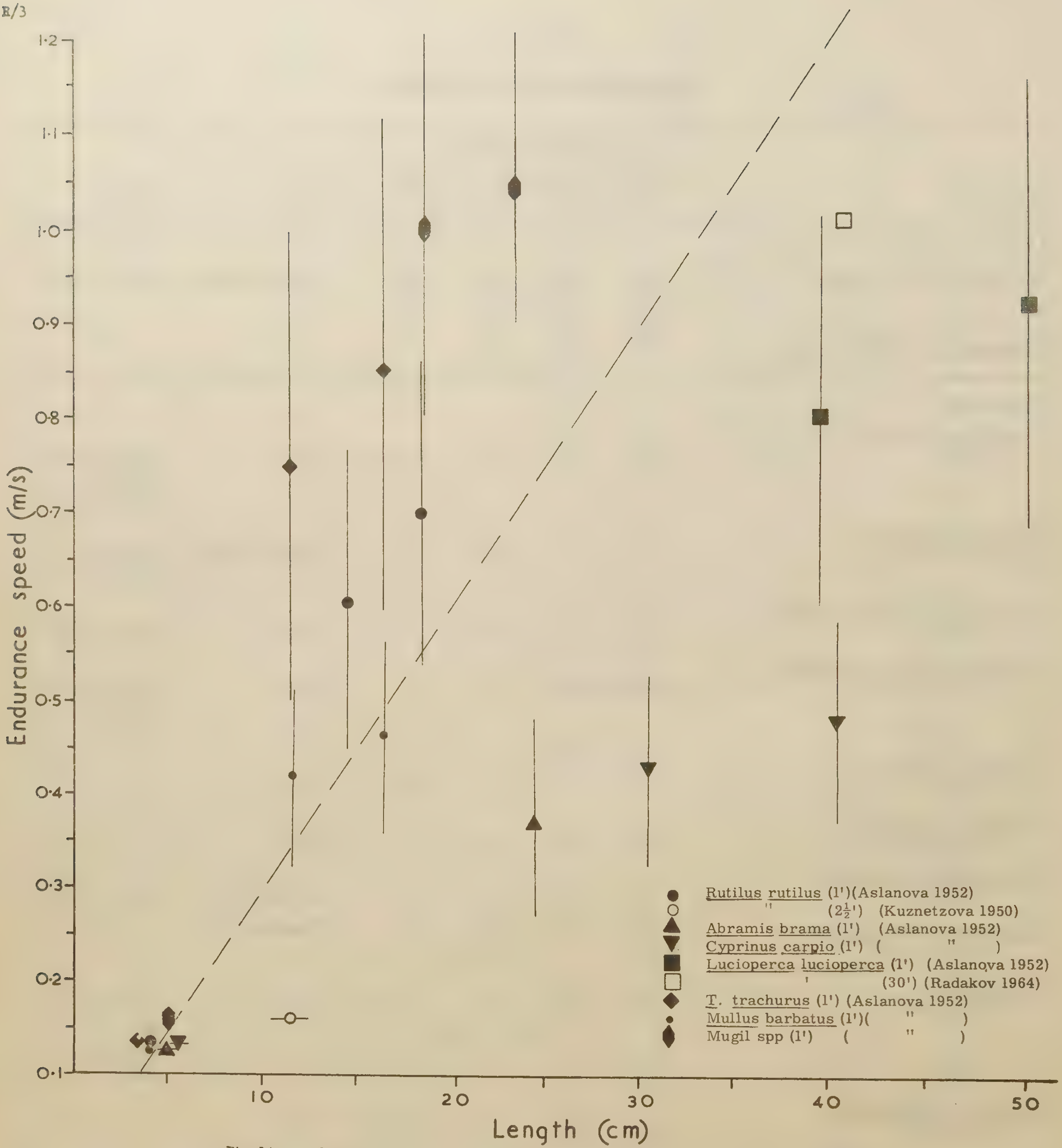

Fig.14 Endurance speeds of certain cyprinids, percids and other species. (mainly from Aslanova, 1952 quoted by Radakov, 1964); see key for times in minutes.

Yuen (1966) related V in body lengths/s to tail beat frequency in beats/s in two tuna species and similarly Magnuson and Prescott (1966) for bonito, as follows:

for skipjack $V = 2.053 + 0.479\ f$

for yellowfin $V = 2.446 + 0.567\ f$

for bonito $V = 0.491 + 0.639\ f$

Blaxter and Dickson (1959) derived the following formula for herring:

$V = 7.6\ L^{0.94}$ where V = speed in cm/s and L is length in cm.

As already mentioned Blaxter and Dickson (1959), Brett (1963, 1964) and Beamish (1966a) concluded that temperature effects on burst speeds were not very significant. This may be due to high temperatures in the muscles during intense activity making the fish, to some extent, independent of the ambient temperature. Certainly Fukushima (1952) found in skipjack tuna muscle temperatures considerably above ambient.

With regard to endurance or cruising speeds there is fairly wide agreement that 2 to 3 B.L/s can be maintained in many species for long periods, even up to 1 h or more. Salmonids and herring seem capable of sustaining 3 to 4 B.L/s or even more for such periods. There are considerable effects of temperature on cruising speeds with optimum conditions within the temperature range and a reduced performance on either side of the optimum. In relation to length Brett (1965) in particular found a reduction in relative cruising performance of O. nerka with age, expressed as: $V = 1.29\ L^{0.5}$ where V = speed in cm/s and L = length in cm. The ability to sustain periods of swimming is proportional to $L^{1.09}$ in dace and $L^{0.65}$ in trout and goldfish (Bainbridge, 1960).

Some idea of relative differences in performance between species are shown in Table II where body-lengths swum to exhaustion at fairly high speeds have been taken or inferred from two publications. There is a tendency for stamina to drop with increase of size (see also Fig. 11) and for herring (shoaling) sea trout (migrating) and winter flounder to have greater stamina than the other species. Sundnes (1963) gave no figures for length of the species for which he calculated endurance. Assuming a fairly high speed of 2 m/s for each of his species it can be seen that cod would swim theoretically about 400 m, coalifish 600 m, pollack 500 m, salmon 600 m, mackeral 300 m, herring 300 m and plaice 300 m. Assuming these fish were of commercial size the herring and plaice, in terms of B.L/s, might show an equivalent or greater stamina than the other species, but there is not the difference in performance detectable which has been found by experiment.

6 BIOCHEMICAL BACKGROUND

Because of the observed behaviour of fish to a towed net, stamina may well be a more important concept than maximum speed, so long as the towing speed is below the maximum speed of the species. Certain histological differences and biochemical changes have been investigated in relation to stamina and maximum speed and these may be briefly referred to.

Boddeke et al. (1959) examined the musculature of a number of species of freshwater fish, considering them from body form, behaviour and swimming performance

Table II

Distance swum at fairly high speeds before exhaustion

Species	Ave. length cm	Body lengths swum to exhaustion	Temp °C	Author
Clupea harengus (herring)	20-25	1121	11-12.5	Blaxter and Dickson (1959)
Gadus morhua (cod)	12-14	151	9-11	"
	48-56	128	10-11	"
Melanogrammus aeglefinus (haddock)	40	143	14	"
Merlangius merlangus (whiting)	15-18	254	9-13	"
Pollachius virens (coalfish)	14-21	293	9-14	"
Pseudopleuronectes americanus (winter flounder)	20-22	600	5-14	Beamish (1966)
Salmo trutta (sea trout)	22-23	975	13	Blaxter and Dickson (1959)
	32-36	496	15-18	
Scomber scombrus (mackerel)	35-36	293	16-17	"
Sebastes marinus (redfish)	16-17	400	5-11	Beamish (1966)

as "sprinters" or "stayers". The sprinters had a higher proportion of white muscle and the stayers of red muscle. Bone (1966) has recently summarised the information on these two types of muscle (with particular reference to the dogfish Scyliorhinus). Apart from differences of innervation and histology the following characteristics were listed in this species:

Red muscle	White muscle
More glycogen	Less glycogen (50 to 60% of red)
Little change of glycogen level with exercise	Level of glycogen falls with rapid movement
More fat	Less fat (20 to 25% of red)
Myohaemoglobin present	Myohaemoglobin absent
Aerobic metabolism mainly	Anaerobic metabolism
For slow movement	For fast movement
18% of total muscle	82% of total muscle.

In addition, the temperature of the red muscle may be especially high; in skipjack tuna Katsuwonus pelamis (Fukushima, 1952) a temperature 5.9°C above the water temperature was recorded. In teleosts generally red muscle is superficial and white is in an underlying mass of much greater volume. In salmonids there may be considerable intermingling of the two types of fibre.

Biochemical changes in blood and muscle with exercise have been extensively studied in salmonids (e.g. Connor et al., 1964, Black et al., 1966). Work has also been done on yellowfin tuna Neothunnus macropterus and skipjack tuna Euthynnus (Katsuwonus) pelamis by Barrett and Connor (1962) and on haddock Melanogrammus aeglefinus by Beamish (1966b). These latter authors also summarise the literature generally. Measurements of lactic acid in the blood and glycogen in the muscle show that little glycogen is used in slow swimming, when aerobic metabolism of fat seems to be the main source of energy. During strenuous exercise there is a very rapid depletion of muscle glycogen and build up of lactic acid in the blood, due to anaerobic glycolosis. In most species the lactic acid changes in the blood seem to follow a fairly consistent pattern. Following strenuous exercise (in the case of salmonids this is often taken as 15 min of fast swimming; haddock were sampled at the end of a 30 min trawl haul at 1.4 m/s) the peak lactic acid level is found not at the end of the period of swimming but 3/4 to 4 h later, the level after exercise rising from 5 to 167 mg/100 ml (depending on the species and condition) to 40 to 278 mg/100 ml. The time to recover the "resting" or unexercised level varies from 8 to 24 h! In the case of glycogen the unexercised level in the muscle may not be restored even in 24 h (Black et al., 1962). In tuna strenuous exercise of only 6 to 21 sec is required to give rise in lactic acid level of 9 to 33 times the unexercised level ½ to 3/4 h later. However, in yellowfin tuna the base level may be reached again in only 1½ h, perhaps due to good circulation and continuous swimming during recovery.

The experiments show that short-lived strenuous exercise may have a marked and long-lasting biochemical effect on the fish. The extent to which this may interfere with subsequent periods of violent swimming or escape reactions is only known with any certainty in salmonids, where additional criteria of activity of respiration have been applied. Paulik, DeLacy and Stacy (1957) found recovery of exhausted coho salmon (O. kisutch) was only 67 percent complete after 3 h, perhaps 5 h being required for complete restoration to the original level. Paulik and DeLacy (1958) observed a considerably poorer locomotory performance of sockeye (O. nerka) after exercise. Hochachka (1961), using rainbow trout, found that pre-exercise levels of glycogen were not restored within 18 h of strenuous activity and respiration rates required 4 to 6 h to be re-established at the pre-exercise level. Brett (1964) working with sockeye found a return to spontaneous activity and near-standard respiration rates about 3 h after exhaustion. It is clear then that fish can build up a considerable oxygen debt and dissipate it later over a long period.

Connor et al. (1964) applied these experimental techniques to observations on salmonids (O. tshawytscha, O. nerka and S. gairdneri) in experimental fish ways with gradients of 1 in 8 and 1 in 16 ascending to 1000 ft. While blood lactate showed a rise of ½ to 2½ times in the first 100 ft in all species, muscle glycogen did not decrease over the first part of the 1 in 16 ascent, though it did in the 1 in 8 ascent. These authors concluded that the degree of exercise over the complete ascent could only be considered as "moderate" and suggest that the fish might have acquired some learnt ability for finding their way by routes of minimum velocity up the fish way, presumably with the most efficient expenditure of energy. Osborne (1961) reached a similar tentative conclusion from his comparison between the movements and fat consumption of Pacific salmon in the Columbia and Amur rivers and the theoretical power required of a rigid "unrefuelled vehicle" moving over the same distance. He found that the fish had a superior performance due perhaps to seeking of low-velocity water, the ability to maintain laminar flow over the body surface or the ability to extract energy from eddies in the river.

There is some evidence in coho and chinook salmon (Parker and Black, 1959; Parker, Black and Larkin, 1959) that hyperactivity causes death; high lactate values in the blood may well contribute to other potentially lethal factors associated with capture. The interesting suggestion is made that adult coho in freshwater are incapable of lethal hyperactivity - due to lack of feeding, carbohydrate values are so low that energy must be obtained from more slowly-mobilised fat and protein reserves. Lactate levels never reach the high values found in the sea after exercise. Lack of carbohydrate may then act as a pacemaker, preventing over-activity in freshwater.

7 HYDRODYNAMICAL BACKGROUND

Some of the anatomical and hydrodynamical features in the swimming of fish have been considered by Gero (1952), Bainbridge (1961), Nursall (1962) and Walters (1962). Of great importance is the type of flow over the surface of the fish. Laminar flow will give a reduced drag, turbulent flow a higher one (perhaps by the order of ten times). Much time has been devoted to discussion on the type of flow and drag, relating this to muscle power and swimming speed. Fish which have good hydrodynamical qualities are broadest and deepest far back along the body (e.g. scombrids). This delays the breakaway or separation of the boundary layer and resultant dead water (and increased drag) at the posterior end of the body. Rosen (1962) succeeded in observing the flow of water of a swimming fish by the use of tanks with a layer of milk at the bottom. He found a series of vortices produced near the gill region against which the more posterior regions of the fish might have been reacting, so extracting energy from the surrounding water.

Some fish apparently have devices to reduce drag (Bainbridge, 1961; Walters, 1962; Ovchinnikov, 1966). In scombrids, which keep the mouth and operculum open, boundary separation may be delayed by the operculum acting as a "leading edge slot". Similarly the keeled peduncle may act as a low-drag coupling for the caudal fin and the caudal keels as boundary layer "fences". The "corslet" or collar of thickened epidermis in the Cybiidae, Thunnidae and Katsuwonidae may cause turbulence in the boundary layer and prevents its separation. In other species it is possible that exhalant water from the gills has the same effect. In the swordfish Xiphias and sailfish Istiophorus which apparently have a very high swimming speed though poor hydrodynamic qualities, the greatest height and depth of the body are anterior. It may be that the rostrum in these species causes turbulence within the anterior boundary layer at low speeds which would delay the separation of the layer posteriorly.

One of the great problems is to measure drag in a moving fish, though many measurements have been made of the drag of models and anaesthetized or dead fish (e.g. Gero, 1952; Sundnes, 1963) and of live fish decelerating without swimming movements. Brett (1963), from measurements of oxygen consumption in different velocities of water, compared the power requirements for live swimming fish with theoretical values obtained from drag measurements on dead ones. He found that the power required to sustain a live fish at 4 B.L/s was 2.2 times less that of a dead fish. At higher and lower speeds this ratio decreased (see Fig. 15). This confirms the view of many workers that drag in a swimming fish is less than that of a rigid specimen. Thus the swimming movements themselves reduce drag. It is unlikely that mucus (Gero, 1952) or a specialised flexible body surface as found in dolphins (Kramer, 1960) plays any significant role, though in marlin and possibly tuna the structure of the skin is such as possibly to serve such a function (see in Bainbridge 1961).

To Bainbridge (1961) is due the most up-to-date exposition of the relation between power requirements, drag and swimming speed. He derived the following formulae, depending on whether flow was laminar or turbulent over the body surface:

$$V_{lam} = \left(\frac{P\ Wm}{0.085\ L^{3/2}} \right)^{2/5}$$

$$V^{turb} = \left(\frac{P\ Wm}{0.01885L^{9/5}} \right)^{5/14}$$

where Wm is the weight of propulsive muscle, L length and P is the power factor. From a search of the literature he arrived at the following values for P.

Maximum power available $P = 8 - 17 \times 10^5$ ergs/cm/g muscle

Maximum sustainable power available $P = 2 - 14 \times 10^5$ ergs/cm/s muscle

(the range of values depending on temperature)

Using these values he calculated the theoretical swimming performance of fish and related it to measured performance. Apart from barracuda the observed values are all within the theoretical capabilities of the fish. The extremely high values reported for swordfish and sailfish mentioned earlier (25 - 36 m/s) clearly would not fit in with these calculations and require confirmation.

8 SWIMMING SPEED AND NET AVOIDANCE

Clearly burst speeds may be of importance in escaping a trawl, especially near its periphery. Cushing and Jones (1966) report observing such responses. On the other hand reports from divers and observation from films and by camera (see paper by Parrish et al., in this symposium) and from tank experiments (Blaxter and Parrish, 1966), indicate that a major reaction of fish is a steady swimming in front of the groundrope or other parts of the trawl. This may be partly a pseudorheotropic response (Livingstone, 1961) and a question of the balance of stimulation on the two eyes. Springer (1957), Radakov (1962) and High and Lusz (1966), in particular, emphasize the relative tranquility of clupeoids during herding, as long as no sudden stimulus intervenes; this may be a general phenomenon.

R/3

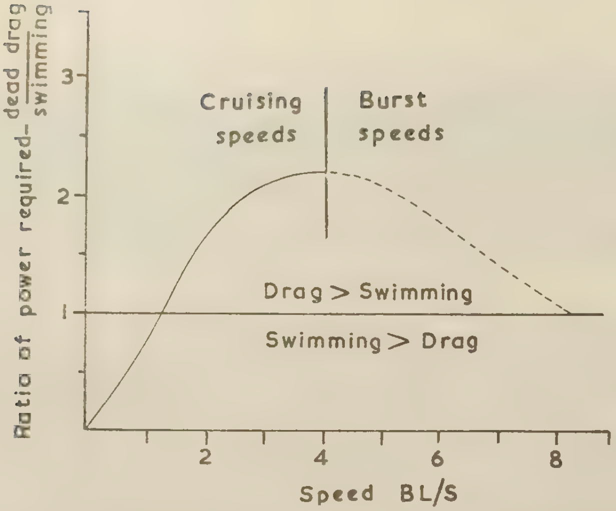

Fig.15 The ratio of power required to overcome dead drag at different speeds to that required for live sockeye salmon. At intermediate speeds living fish need considerably less power than the theoretical amount obtained from drag measurements on dead specimens (re-drawn and adapted from Brett, 1963).

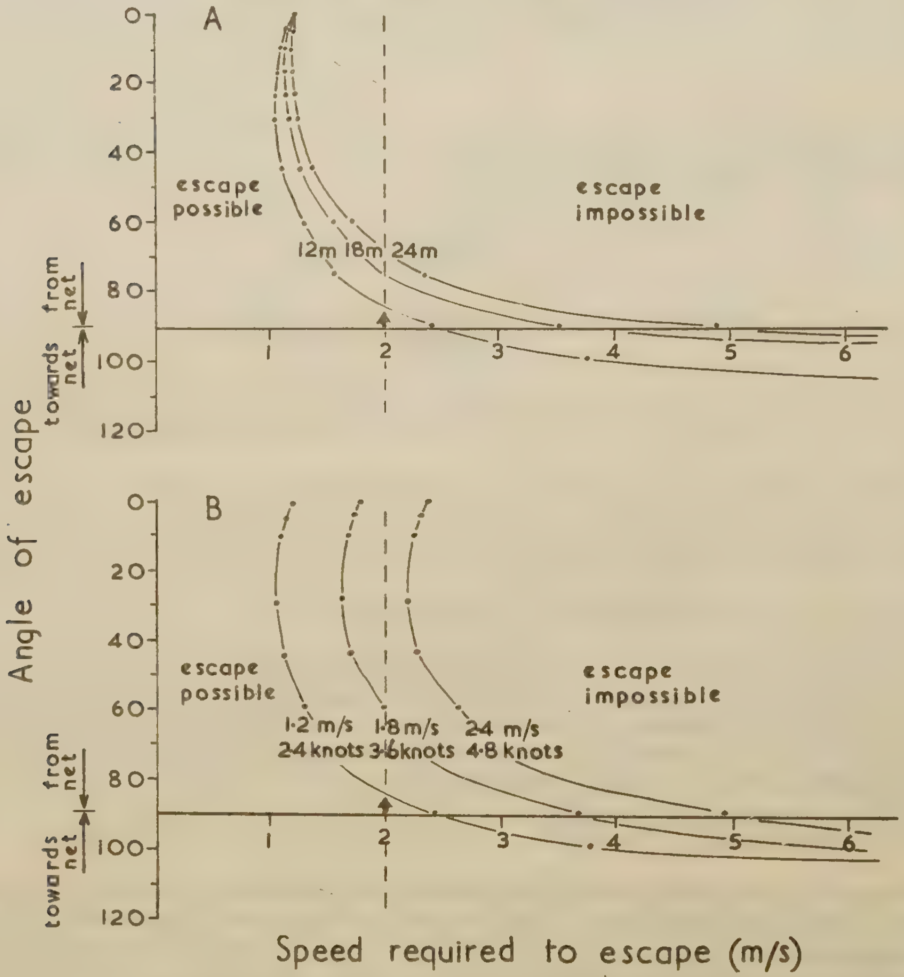

Fig.16 Speed required to avoid a net at different angles of escape when the fish is in the centre of the path of a trawl and reacts 3 m away. Broad arrow at 2 m/s shows maximum burst speed for adult clupeoids.

A. The change in relationship when nets of 12, 18 and 24 m spread are used at a towing speed of 1.2 m/s (2.4 knots).

B. The change in relationship when nets of 12 m spread are towed at speeds of 1.2, 1.8 and 2.4 m/s (2.4, 3.6 and 4.8 knots).

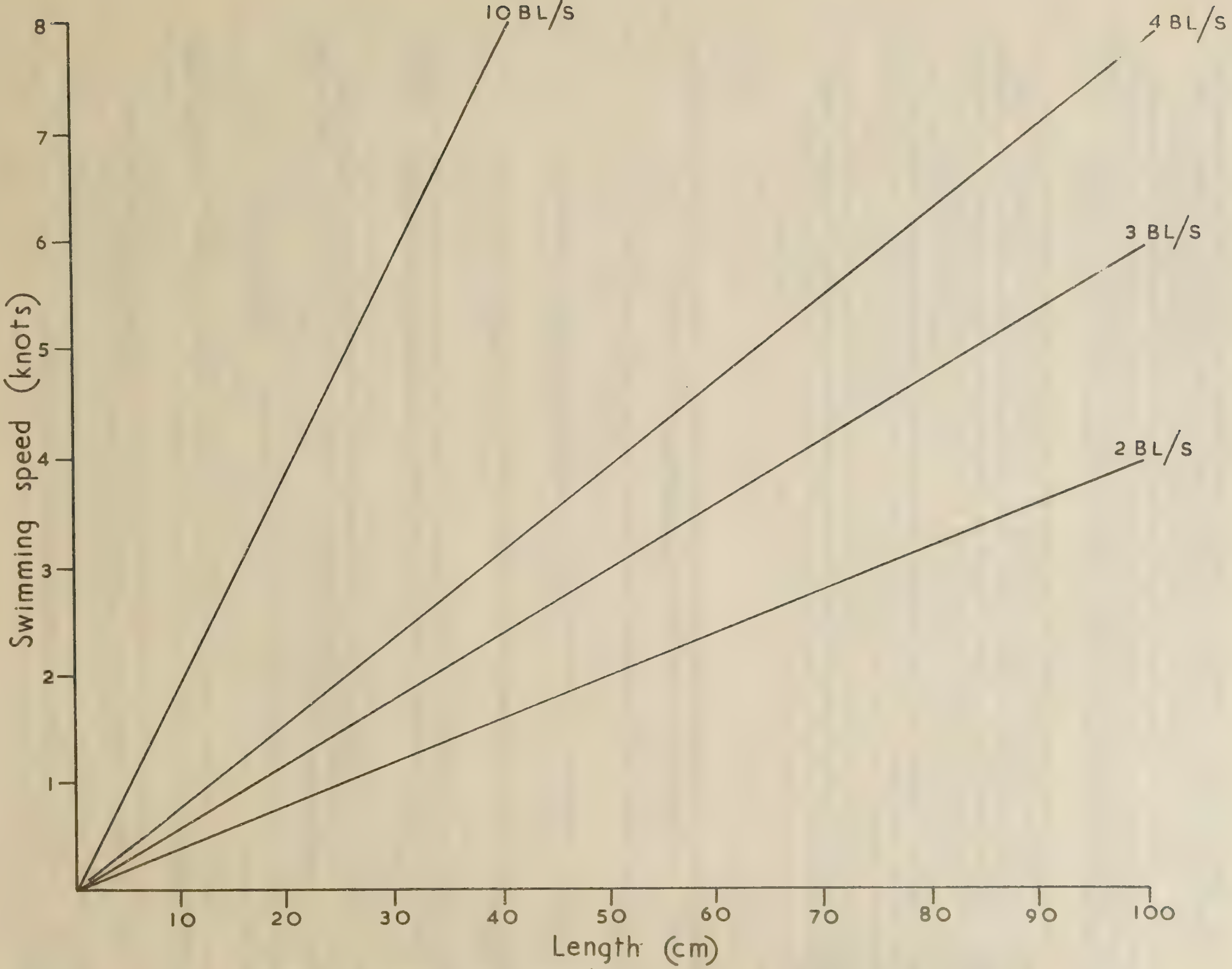

Fig.17 Speeds as body lengths/second for fish of different length converted to knots for comparisons with towing speeds.

The possibilities of escape by burst speeds around the wings may be related to the position of the fish relative to the net when it first reacts, its burst speed, the speed of tow and the size of the net (see Fig. 16). On theoretical grounds, taking any particular burst speed (2 m/s is used for adult clupeoids), the chances of escape diminish more by increasing the speed of tow than increasing the spread of the net. Barkley (1964), on rather similar grounds, considered there was an optimum size and speed of tow to prevent avoidance of a plankton net.

Where fish are being herded before the net the speed of tow relative to the endurance speed of the fish is more relevant. In Fig. 17 cruising speeds of 2,3,4, and 10 B.L/s are converted to knots. For fish of commercial size, above 30 cm, towing speeds of 2 to 3 kn (1 to 1.5 m/s) should be adequate for overcoming smaller fish, except herring, during a haul, but may well be on the low side for larger species or older fish. The ability of a particular net to catch fish must depend, however, on other factors. Because a steady stimulus rather than a changing one is likely to reduce fright reactions, a steady towing speed on smooth ground should prevent escape movements in bursts, the fish becoming habituated to the movement of the net and falling back into it on tiring. Jerky movements and changes in speed would probably mean that the fish remain in front of the net for a longer period. For those fish left at the end of the haul, the "knocking-out" procedure or closing of a Danish seine may represent very critical phases during the process of capture.

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DETECTION OF FISH AND OBSERVATION OF FISH BEHAVIOR BY ECHO ANALYSIS AND PASSIVE LISTENING

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Abstract

Reasons for the need of behavior studies in modern fishing, especially concerning pelagic species, are given. Possibilities, advantages and disadvantages of acoustic means, compared with other observation methods are discussed. The general characteristics of echo sounding and sonar are given and the types of acoustic devices used in fisheries and fishery research are described with special reference to sonar and the netsonde. Examples of the use of sounding devices for identification of fish species and behavior observations are discussed. Also, the effect of ultrasonic energy on fish is discussed. Lastly, the applicability of passive listening for fish detection and behavior studies is described.

DETECTION DU POISSON ET OBSERVATION DE SON COMPORTEMENT PAR L'ANALYSE DES ECHOS ET PAR L'ECOUTE PASSIVE

Résumé

Après avoir expliqué pourquoi la pêche moderne, notamment des poissons pélagiques, exige des études de comportement, l'auteur examine les possibilités, les avantages et les inconvénients des méthodes acoustiques par rapport aux autres méthodes d'observation. Il donne les caractéristiques générales du sondeur à ultrasons et du sonar, et décrit les types d'appareils acoustiques employés pour la pêche et pour la recherche halieutique, en s'attachant particulièrement au sonar et au "netzsonde". Il cite des exemples d'emploi de dispositifs de sondage pour l'identification des espèces et les observations sur le comportement, et examine l'influence de l'énergie ultrasonore sur le poisson. Enfin, l'auteur décrit les possibilités d'application de l'écoute passive à la détection du poisson et aux études sur le comportement.

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DESCUBRIMIENTO DE PECES Y OBSERVACION DE SU COMPORTAMIENTO MEDIANTE ANALISIS DE ECO Y ESCUCHA PASIVA

Extracto

Se exponen las razones de la necesidad de llevar a cabo estudios de comportamiento en la pesca moderna, especialmente sobre las especies pelágicas. Se examinan las posibilidades, ventajas e inconvenientes de los medios acústicos con respecto a otros métodos de observación. Se indican las características generales del sondeo por eco y del sonar, y se describen las clases de instrumentos acústicos empleados en la pesca y en las investigaciones pesqueras, con especial referencia al sonar y a la sonda para redes. Se examinan ejemplos del empleo de instrumentos sonoros para la identificación de especies de peces y observaciones sobre su comportamiento. Se examina igualmente el efecto de la energía ultrasónica sobre los peces. Por último, se describe la aplicabilidad de la escucha pasiva para el descubrimiento de peces y los estudios sobre su comportamiento.

1 INTRODUCTION

Fish detection and knowledge of their behavior during capture have become critical factors in successful modern fishing. In the last two decades fisheries have increased in all parts of the world, and competition between fishermen, fishing companies and fishing nations has accelerated markedly. As a result, more effective and sophisticated fishing techniques have made many traditional methods unprofitable. Because of the intense fishing, many stocks - especially those of groundfish - have decreased sharply. Thus more effective means for fish location have become necessary (Cushing, D.H. et al.,1952).

The introduction of echo sounding for fish detection has been so successful that in spite of decreasing stocks, landings of fish in many cases have increased. This is a trend which of course cannot continue indefinitely. Consequently, in order to provide additional landings of fish, considerable interest has developed in the abundant and less exploited pelagic species. Trials with new gear demonstrated that pelagic species are in general more active and consequently better able to avoid gear than bottom fish. Thus it has become necessary to study the behavior of fish during the fishing operation in order to learn what changes are required in the gear or the method of operation in order to provide an effective harvesting system.

The problem of studying behavior of fish in relation to fishing gear offers no simple solutions. Aquarium experiments, even when conducted in large tanks, may give important clues and detailed information on some behavior patterns, but neither from the physical nor the biological point of view can the conditions prevailing during commercial deep sea fishing operations be approximated.

Observations made with the help of divers and manned underwater vehicles are only possible under favorable weather conditions and relatively near to the surface. The applicability of these methods depends on a sufficient supply of daylight, because artificial light would mask or change the normal reactions of fish to the gear considerably. Also, vision in the sea is usually restricted to a few meters because of the turbidity of the water. These same handicaps apply to underwater cameras and television.

The use of sonic techniques for behavior studies offers advantages and possibilities for effective studies which are not possible with aquarium or visual methods. There are two theoretical methods for acoustic location and observation; passive listening and echo analysis. In passive listening the noises produced by the organisms are detected by hydrophones and recorded on tape. The analyses of these records may give clues as to the species. abundance and distribution as well as on behavior (swimming, feeding, courtship, threatening sounds, etc). In acoustic analysis pulses of sound energy are transmitted into the sea and from the echoes received conclusions are drawn as to the presence and distribution of organisms in the water. This is comparable to the use of electromagnetic energy for the location of objects on the surface or in the air (radar).

The frequencies used for echo sounding in fisheries are a compromise between many requirements, resulting from limitations imposed both by physical laws and technical possibilities. With high frequencies the sound beam is concentrated sharply and the pulse length can be reduced. Consequently, the "resolution" of the system is good and small objects can be detected, i.e., single fish within schools. Also, the transducers are small and therefore relatively cheap. The disadvantages of high frequencies is the high rate of energy attentuation resulting in a relatively short effective range. Yet for special fisheries work in shallow water (shrimp fishing and for scientific purposes) echo sounding units with frequencies up to 400 kc/s have advantages (Cushing, D.H. 1963 and Stengel, H. 1961).

The situation is reversed for low frequencies. Small objects diffract the sound energy rather than reflect it. Consequently resolution of small objects is poor. However, the range is greater the lower the frequency used. When great depths (one thousand m and more) are to be measured or large objects are to be ranged from great distances, sound of the audio frequency range must be used instead of ultrasound. Most sonic equipment used for fisheries purposes produce sounds in the range between 15 and 50 kc/s, which has been found to be the best compromise for commercial fishing.

Sonic echoes are represented basically by three means: "scope" (cathode ray tube) indication, "graph" indication, and audible sound. The most simple "flash" indication can only be used for depth determination. Each of these methods has advantages and disadvantages. Graph recording has the advantage of producing a permanent record, but at the expense of detail. Scope recording gives much more detailed information since the echo strength is faithfully reproduced, but a permanent record is not obtained. In scopes with long image retention features the advantages of both methods are to some extent achieved because the traces fade very slowly (Anon. 1964 and Miers, U. 1967). The movements of fishes are better recognisable with this technique than with any other. For behavior observations a combination of scope and graph indication is nearly indispensible. Indication by audible sound has the operational advantage in sonar searching of earlier detection of fish schools. Also it permits searching without the necessity of constant visual monitoring. Echo sounding and echo ranging were introduced into commercial fisheries shortly after World War II. Since that time most fisheries have become so dependent on one or both of these techniques that they could not exist without them (Nishimura, M. 1966).

Designed and used originally for navigation and fish detection only, it soon became obvious that echo sounding could also be used for gear observations and fish behavior studies. Compared with the optical observation methods mentioned previously, echo sounding has the advantages that illumination is unnecessary and the range is much greater than is possible visually. It can be used in any depth and in all weather and sea conditions where commercial fishing operations are possible. Because ultrasonic equipment is installed on practically all fishing vessels and is used during each fishing operation, behavior observations can be made on a very broad scale. This permits accumulation of large quantities of data which facilitate the separation of rules and exceptions. Moreover, each skipper can make the observations himself, which is usually more convincing than second-hand information. Also, the behavior observations are obtained at little additional cost. Once installed the echo-sounding equipment does not require additional expense in either time or personnel. In addition to their application for fish detection and observation, they are also used for navigation purposes. The most serious disadvantage of echo sounding in fish studies is that the information is much less detailed than that obtained by direct or indirect visual observation. Identification of species is uncertain and usually depends on verification by other means.

In order to get the most information from the echo indications and to avoid errors and misinterpretations, a good knowledge of acoustics, the recording techniques, and considerable practical experience is necessary. Fortunately, excellent and easily understandable introductions to this field are accessible which in a short time give even a novice the knowledge necessary to begin practical application of the equipment (Cushing, D.M. 1963; Tucker, D.G. 1966 and Anon. 1960).

A great handicap when comparing echograms from different units is the different rate of amplification usually used. A satisfactory calibration of the units seems nearly impossible, although calibration devices are constructed by some firms (Anon. 1965). This is because the factors varying the strength of the traces are numerous and difficult to control since they depend partly on environmental conditions ("sound weather") (Herbst, H. 1965 and Stengel, H. 1961).

2 TYPES OF SONIC ECHO DEVICES USED IN FISHERIES AND FISHERY RESEARCH

The echo devices used in fisheries are customarily classified into horizontal sounders (sonar), vertical sounders (echo sounders) and net sounders (netsondes). The operating principle of the three types is the same and was described earlier. Some have a multipurpose applicability or can at least be used as a substitute for the others. In an effort to avoid confusion of terminology and to standardize descriptions of the three echo devices the terms sonar, echo sounder and netsonde are used in this paper.

The transducers of sonar are attached at the bottom of the ship near the keel to avoid aeration and to facilitate tilting and sweeping in all directions. In sets for large vessels the power output of the transducers is 1 to 5 kW with an effective range up to 2000 to 4000 m. The frequencies used are relatively low (15 to 30 kc/s) because long range detection is more important than detailed resolution. The beam angle is usually 10° to 20° and some units have an additional wide beam for short range detection. Sweeping and tilting of the transducer can be either automatic or manual. The search sector and method of scanning ahead of the ship depends on the speed of the vessel and water depth (Herbst, H. 1965). A Review on the development and present application of echo-sounder and asdic in Norway, from where the use of acoustic instruments for fish detection started after the war, is given by Dragesund and Midttun, 1966. For pelagic trawling it is most important that the transducer be trained directly aft in order to observe the space between the ship and the gear. Some sonar systems do not possess this feature.

In devices for small open boats - especially for the dinghies used in purse seining - the transducers are manually controlled by a simple joystick. The range of these small units does not exceed 500 m and the echoes are recorded only graphically.

An electronic sector scanning instrument has been developed especially for behavior studies (Harden Jones, F.R. and B.S. McCarthy 1962; Tucker, D.G. and V.G. Welsby 1964; and Anon. 1966). In this design many transducers are used which present indications on a scope comparable to a movie. Because this device is covered by another paper at this meeting it shall only be mentioned here.

Temperature and salinity variations within the water column make accurate interpretation of sonar echoes more difficult than is the case in depth sounding. In shallow water, sonar is often useless due to reflections from the bottom and surface (Haines, R.G. 1958 and Herbst, H. 1965). Echo signals are usually represented both graphically and by a loudspeaker. The latter precludes the necessity of constant visual monitoring of the graph recorder. Recently, modern sets have been equipped with a scope display also. A comprehensive description of the use of sonar in fisheries has recently been published by Tucker, D.G. 1967.

The echo sounder was the first echo device used in fisheries and is still the most common sonic instrument in use. The transducers are fixed in the hull near the keel to avoid signal interference due to aerated water adjacent to the transducer face. The frequencies used for sounding in commercial fishing operations are usually in the range of 30 to 50 kc/s. The effective distance range is 200 m to 1000 m and the usual beam angle is 30° to 60°. For commercial fisheries a very narrow beam is impractical because as the ship rolls, the sharply concentrated beam points alternately from side to side giving an undecipherable mixture of indications of depth and fish traces. For scientific investigations, especially stock assessment, when a very narrow beam angle is necessary (down to 2°), the transducer must be stabilized by using gyroscopes (Anon. 1965). The echo indications are represented graphically and/or by a scope. In order to obtain as accurate an interpretation as possible, graph and scope recordings are used simultaneously in modern echo sounding units.

The net-sounder or netsonde are terms sometimes used to describe various sonic instruments which are secured to a trawl. These include instruments for sensing various parameters as well as for sonic transmission of information to the vessel. The netsonde system of widest application in commercial fishing and behavior studies consists of a sonic transducer mounted on the headrope and connected directly to the shipboard recording system by an electrical cable. This system is used primarily in pelagic and near bottom trawling. In bottom trawling the risk of losing or destroying the device is much greater and the opening height of the net is usually so small that the "zero sound" of the recording almost completely covers the net opening indication. Also, on hard bottom noise from the bobbins creates severe interference with the desired signals.

In addition to the netsonde, various instruments are mounted on the trawl or doors for sensing environmental parameters such as depth of the instrument and water temperature. These do not relate directly to behavior studies and consequently are not considered here.

The standard netsonde is usually mounted at the center of the headrope with the sound beam directed vertically downward. In this mode of operation the footrope echo, the bottom echo and fish within or under the trawl mouth are recorded. Control of the trawl depth to intercept schools detected by either sonar or echo sounder aboard the vessel is possible as is observation of the behavior of the fish in relation to the trawl. In situations where the distance from the transducer to the bottom is greater than the depth range of the instrument the depth of the trawl cannot be measured. In this case sometimes the sound-proof shield on the top of the transducer is removed. This results in simultaneous downward and upward signals with the upward signal providing an echo from the surface and consequently the depth of the trawl. This solution, although helpful in many instances, has the major disadvantage that the origin of fish echoes is not detectable - except in cases where they demonstrate a pronounced reaction to the footrope and thus must be below it. To overcome this difficulty, some netsondes have a directional capability designed into them. These units are capable of remote switching of the transducer between downward, upward and forward directions (Miers 1967 and Anon. 1967). Quite recently in Japan a net-sounder without cable was developed, which gives detailed information on the presence of fish in the netmouth and below the net too. It consists of a transmitter unit, sending signals on a frequency of 200 Kcps, but transmitting the echoes received on 50 Kcps to the receiver unit, which is towed on a cable astern of the vessel. (**Anon. 1966**).

For scientific observations more detailed information than is possible with a standard netsonde system is desirable. This can be achieved by using more than one transducer on the headline (Margetts, A.R. and J.P. Bridger 1967) and/or at other locations on the gear (Schärfe, J. 1966 and Schärfe, J. 1967). A scope display with a long signal retention feature used in conjunction with multiple transducers is very useful for obtaining accurate information on trawl avoidance parameters such as swimming speed and direction.

The cost of sonic equipment required for the various purposes described is rapidly rising as the units become more versatile and sophisticated. To minimize this disadvantage recording units which accommodate signals from both the echo sounder and the netsonde have been developed. Also, in fleet operations sometimes only a few ships are equipped with sonar. These ships conduct long range search patterns and pass information to the fleet (Herbst, H. 1965). Government research vessels sometimes perform this searching service for fishing vessels of their country.

3 BEHAVIOR OBSERVATIONS REVEALED BY ECHO SOUNDING

In any animal behavior study it is necessary to identify the species involved. As mentioned above, this is difficult when studying fish in the sea with sonic methods and usually must be verified by additional observation techniques such as diving, photography and television.

In the case of commercial fishing the actual proof is the catch. However, fishermen usually want to know before shooting the gear which species is indicated. The strength of the echo gives some clues to this. Species which have a swimbladder or a hard body are better echo producers than soft fish and fish lacking a swimbladder, and the echoes of large specimens are stronger than those of small ones. These differences can usually be seen distinctly, especially on a scope, where the echo strength is faithfully reproduced. Work is underway to develop an echo sounder with continuous modulated sound transmission. A complex sound analyser will sort the echo returns and classify them. These data, when represented on a cathode ray tube, shall make it possible to tell even an albacore tuna from a skipjack tuna (Anon. 1965).

More than the differences caused by physical properties, features of behavior, especially shoaling patterns, may give clues to the identification of species. Traces of fish shoals, especially of migrating fish, usually have a sharp and distinct border, whereas the edges of plankton concentrations are always fuzzy. To distinguish layers of fish from those of jelly fish an object imitating a predatory fish can be cast in the water or lowered on a rope into the beam of the echo sounder. Fish will keep clear of the object, jelly fish will not (Spectorov, M.J. 1961). The diurnal vertical migration of fish differs widely in extension and time from species to species, which can be observed excellently in the echo sounder and thus gives a good indication of the species.

In addition to these general behavior patterns fish can sometimes be identified by their reactions to the gear. In the representation on the echo sounder, shoals of sprat and herring cannot be distinguished, but on the netsonde it is seen that herring usually react very strongly whereas sprat do not react to the approaching net (Mohr, H. 1964 a and Mohr, H. 1964 b). Blue whiting and herring are difficult to distinguish on the echo sounder, but can often be identified by the response pattern to the gear which is similar to that of sprat.

Like most behavior patterns, schooling and reaction to the gear depend on many intrinsic (maturity stage, hunger, etc.) and extrinsic (hydrographical conditions, light conditions) factors. Thus observations and experience are only transferable and applicable under the same conditions.

The examples mentioned above indicate that for observations during the process of catching the combined use of different sonic instruments is profitable and sometimes necessary. The reactions to the gear are restricted in time and space consequently it is necessary to compare the distribution of the undisturbed fish prior to encountering the trawl with their response to it as it approaches.

When observations of the behavior of fish are made by research vessels, auxiliary boats equipped with sounding devices can be used to observe the reaction of the fish towards the gear (Mohr 1964 b) or multi-sounders, i.e., transducers fitted on warps, bridles, wings, ground and headrope or in the net, may indicate the distribution of fish at these places. This effort would be too expensive in commercial fisheries, but when special research succeeds in finding reliable rules in the reactions of fish and thus can give proposals for the construction and handling of the gear it can be of considerable value to commercial fishing operations.

In some fisheries the observation of the reactions to the gear is so essential to success that each captain must observe the behavior of the fish himself during the fishing operation by echo devices in order to operate the fishing gear effectively. This is especially the case in pelagic trawling and in purse seining. Due to their importance and because the use of sonic equipment is most advanced in these fisheries, the application of the different echo devices during fishing will be discussed in greater detail.

A modern midwater trawler is fitted with a sonar, one or two echo sounders (preferably of different frequencies for use according to the prevailing conditions) and a netsonde. When an acoustical or graphical indication of a fish school is received by the automatically scanning sonar, the school is located by manual scanning and the vessel sets course for it. In addition to the distance, estimations on size, concentration, swimming speed, and swimming direction are obtained by the indications of the sonar (Miers, U. 1967). When the vessel has reached the school, the vertical distribution is determined with the echo sounder and the depth of the net is adjusted according to the densest spot of the school. If the gear is still aboard, the vessel must come clear of the school before shooting the net. In this case a sonar is most effective for monitoring the school location. When the vessel has passed over the school the location of the fish is monitored with the sonar directed aft, so that vessel course changes can be made in the event of the school changing position. If the net sounder is equipped with a transducer directed forward, the fish and their reactions can be seen before the net has reached them. If they succeed in swimming at towing speed, the speed of the vessel must be increased. When the fish are in the net mouth, being indicated by the vertically directed transducer on the headline, they may swim with the trawl for a long time and give false indications of a large catch. However, from the traces on the echograms and especially on the scope with a storing screen, it can usually be determined whether the fish are swimming with the trawl or passing into the net. Only when the traces indicate that a satisfactory catch has been obtained is the gear hauled.

In the case of purse seining, different types of sonar are the most important sounding devices. When a shoal is located with the sonar the vessel approaches to within about 500 m because schools close to the surface will usually sound when a vessel passes over. This is especially true for herring. After approaching the school, a small dinghy fitted with a short range sonar is swung overboard and the school observed in some detail (Gerhardsen, T.S. 1959 and Anon. 1966). The seiner is then contacted by radio and, based on the information obtained from the dinghy, the purse seine set is made. When the school has been surrounded by the seine, the sonar is switched off and the still open section of the net beneath the vessel is observed with the echo sounder to determine if fish escape.

4 DOES ULTRASONIC SOUND FRIGHTEN FISH?

Since echo sounders were introduced in fisheries, there has been a question of whether or not the sound transmitted frightened the fish. The fact that whales and porpoises react strongly to ultrasonic sound and that their fear to pass through a sound beam is used for their capture strengthened the suspicion. Fish are frightened by noise, as mentioned in the case of purse seining, but most fish react only to noise of low frequencies. In aquarium experiments, no fish were found to hear frequencies higher than 13 kc/s of moderate sound pressure (Busnel, R.G. 1963). No reactions to ultrasound emitted by echo sounders used in fisheries have been observed (Mohr, H. 1966, Schärfe, J. 1951 and Skoglund, G. 1963). In few cases it seems that fish have exhibited conditioned responses to ultrasound (Bull, H.O. 1961). Most probably these acquired reactions were due to an audible by-sound produced in inefficient echo sounders (Mohr, H. 1966). In commercial fisheries these by-sounds would have no effect on fish behavior because they would be masked by the ship's noise. Only ultrasound of extremely high sound pressure is known to cause reactions or to be harmful to fish and other organisms (Rumiantzev, A.J. 1960), and can be used for scaring them (Anon. 1964). Though neither innate nor conditioned reactions by fish to ultrasound emitted by fish-finders have been proved, an indirect reaction is reported for tuna which were associated with porpoises. In these schools, when the porpoises sensed the ultrasound beam they sounded, and the tuna followed them immediately (Anon. 1962).

5 PASSIVE LISTENING

Passive listening as a means for detecting fish has been known in some fisheries for many years. The conditions for application of this method are that the fish concerned produce noise, and the environment is relatively quiet so that these noises can be detected. These conditions are best realized in tropical and subtropical waters. In the Indo-Pacific area use is made of acoustical detection and identification of fish as an aid in the fishing operation (Steinberg, R. 1957 and Westenberg, J. 1953).

In temperate and arctic zones, the most important centers of commercial fisheries, passive listening is severely handicapped for various reasons. The number of species producing sounds is smaller; the almost constant wave action creates a high level of ambient noise (background noise); and all fisheries are conducted with motorized vessels which mask fish sounds. For example, the sound pressure of most fish noises is in the range of 10 - 35 db re 1 µb at about 1 m distance from the sound source. At a distance of 150 m the noise produced by a trawler is greater than 40 db and therefore disturbs passive listening for many miles (Freytag, G. 1964).

The production of sound by fish became of military interest during the last war when it was learned that fish were producing noises which were confused with submarine noises (Tavolga, W.N. 1964). Consequently, scientific studies of noise production by fish were initially conducted or financed by military organizations. The application of some of the information acquired and equipment developed to commercial fisheries has been a logical extension of this effort.

The hydrophones used in passive listening are of two major types: dynamic systems which utilize vibrating diaphragms, and crystal systems which use the piezoelectric effect of certain crystals. For bio-acoustical investigations the sensitivity of the transducers range between -70 db to -90 db re to 1 V. 1 µb. Most important with respect to their usefulness is the linear performance in the audio spectrum, the temperature stability, the directional pattern and the capacity. The noises received are monitored with loudspeakers or headphones and are also usually recorded on tape for future analyses. Because the development of some special hydrophones is largely controlled by the military, availability to fishery scientists of some desirable hydrophone designs is restricted.

To bring a certain order to the variety of fish noises they may be divided by their origin and meaning into "mechanical" noises, which occur accidentally during feeding, swimming, breathing, etc. (Moulton, J.M. 1960, and Lanyon, W.E. and W.N. Tavolga 1960), and "biological" noises produced by special or specialized organs (stridulatory mechanisms and accessory muscles at the swimbladder). These noises are produced purposely for intraspecific or interspecific communication (Fish, M.P. 1957). Another reason for categorizing the nature of fish sounds is to distinguish harmonious and unharmonious noises (Freytag, G. 1967 and Tavolga, W.N. 1964).

Because the characteristics of most noises produced by marine animals are initially unknown the same difficulties as mentioned for echo sounding are encountered in their specific identification. Initially tests were conducted in aquaria and the fish induced to produce noises often by quite unbiological stimuli. The noises were recorded and analysed as to characteristics of frequency, sound pressure and rhythm. In this way an attempt was made to establish a catalogue of all possible noises occurring in the sea (Fish, M.P. 1954). Unfortunately, recent investigations have shown that a common aquarium distorts sound characteristics to such an extent that it is impossible to recognize the same sound source when similar tests are made in the field (Freytag, G. 1967). Consequently aquarium records are of little value as a means for primary identification of fish sounds. In order to obtain accurate records it is necessary to work in the natural habitat of the fish. Sound studies in the natural habitat have been made using hydrophones for listening and closed circuit television for observation. Both systems were monitored from land stations (Tavolga, W.N. 1964). As yet there has been no use of hydrophones in commercial fishing, though some of the most important fish such as cod, haddock, and herring have been shown to be, at least seasonably, fairly intense noise producers (Brawn, V.M. 1961; Hawkins, A.D. and C.J. Chapman 1966; Freytag, G. 1961; and Hering, G. 1964). The disturbances by the fishing vessels are too big a handicap. In a Russian publication about acoustic possibilities in fish location some methods described for overcoming these difficulties are: stationary hydrophones, which automatically sweep to the direction of a noise caused by a fish school; hydrophones connected by cable with a helicopter; and hydrophones suspended on buoys and fitted for radio transmission to aircraft (Protassow, W.R. 1965).

Apart from their use for fish detection and location, hydrophones can be used for somewhat different purposes in fisheries. In Japan the chambers of large set nets have been fitted with hydrophones which were monitored by a radio system from a land station. It demonstrated that the intensity of the sound detected was a very good measure of the amount of catch. This method permitted timely lifting of the net and consequently the system was more effective than set nets not equipped with hydrophones (Hashimoto, R., M. Nishimura and Y. Maniwa 1960). A further possibility, which goes beyond passive listening, would be the playback of recorded fish sounds in order to attract fish of the same species (or their predators) and thus concentrate them for capture (Moulton, J.M. 1956).

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THE USE OF ECHO SOUNDERS AND SCANNERS IN THE STUDY OF FISH BEHAVIOUR

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Abstract

Methods of interpretation of information obtained by echo sounders and scanners to yield reliable criteria for study of fish behaviour are discussed. To overcome limitations of echo sounding in fish behaviour studies, a statistical basis for analyzing echo sounding observations is described. Also, the importance of relating exact laboratory experiments with extensive observations at sea is stressed.

UTILISATION DES DISPOSITIFS DE SONDAGE OU DE BALAYAGE A ULTRASONS DANS L'ETUDE DU COMPORTEMENT DU POISSON

Résumé

L'auteur examine les diverses méthodes d'interprétation des données fournies par les dispositifs de sondage ou de balayage à écho permettant d'obtenir des critères dignes de confiance pour l'étude du comportement des poissons. En vue de compenser les limitations du sondage ultrasonore dans le domaine des études de comportement, il décrit une base statistique pour l'analyse des observations faites par cette méthode. Il souligne également combien il importe de compléter les expériences précises de laboratoire par de nombreuses observations en mer.

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EMPLEO DE ECOSONDAS Y ECOTELOMETROS DE EXPLORACION EN EL ESTUDIO DEL COMPORTAMIENTO DE LOS PECES

Extracto

Se examina la manera de interpretar la información obtenida mediante ecosondas y ecotelómetros de exploración para obtener criterios fidedignos para el estudio del comportamiento de los peces. Se describe un método analítico para analizar las observaciones de las ecosondas que vence las limitaciones de éstas en el estudio del comportamiento de los peces. Se menciona la importancia de relacionar experimentos de laboratorio exactos con observaciones extensivas realizadas en el mar.

1 INTRODUCTION

A typical chart from an echo sounder appears to be a section of the ocean, showing the distribution of fish in great detail from the surface to the bottom. So, changes in the distribution with time are readily interpreted as consequences of changes in behaviour. There are two drawbacks to this procedure. First, fish traces can only be identified by capture, and therefore study should be limited to the depth zone within which the catching gear operates. Secondly, an echo chart is deceptively simple, needing considerable experience in its interpretation; for example, the lack of fish below a given depth does not mean that they are not there, unless it can be shown at the same time that the echo sounder has the power to detect them. This paper is concerned with the methods of interpretation and with the reliable information on behaviour that emerges.

2 INFORMATION GIVEN BY AN ECHO SOUNDER

Fish appear on an echo chart either as single fish or as shoals. To study behaviour, the resolution of shoals into masses of discrete individuals is obviously desirable. This end is achieved with high frequency (100 to 500 kHz) sounders using narrow beams and short pulse lengths. However, shoals are often recorded and must be considered.

2.1 Single fish

2.1.1 Directivity and the mean angle of the beam θ_m The beam of the echo sounder in angle θ extends from the axis of transmission to the first minimum, θ_{min} (for most purposes, the side lobes can be ignored; but not within a short range of the transducer). Between the axis θ_0 and θ_{min}, the transducer has a characteristic directivity pattern, 100 percent at θ_0 and zero at θ_{min}, described in the curve of $(\sin x)/x$. Between θ_0 and θ_{min} the numbers of fish increase with angle θ as the square of the angle θ. There are two distributions in angle θ, directivity decreasing with increasing angle and numbers of fish increasing with increasing angle. The product distribution peaks at a middle angle, θ_m.

If single fish are being recorded, they can be averaged in time from any range shell. Hence, the average in range or signal strength can be regarded as being received from θ_m for a period of time. The distribution about θ_m is complex. Thus for any range shell the information can be considered as being received from the mean angle, θ_m.

Signals from a single fish are received for a number of transmissions and the volumes from which the fish are sampled overlap. The sampling volume varies with size of fish and ideally should be specified for the size of fish when it is counted. Then the numbers recorded per unit time are considered as being received from that specified volume. This problem is discussed in more detail in Cushing (1967a).

2.1.2 Depth It follows from the previous section that the depth of an individual fish trace is overestimated and, within 5 to 10 percent, indeterminate. However, if observations are averaged within a range sector from fish for a number of fish during a time period,

$$Z = R.\cos \theta_m$$

where R is the average range (or average apparent depth on the paper record), and Z is the true depth. Hence, given good estimates of R in each range sector, reliable depth distributions can be obtained. It should be realized that the overestimate of depth (R) varies with range and so even a relative distribution in depth can be biased slightly.

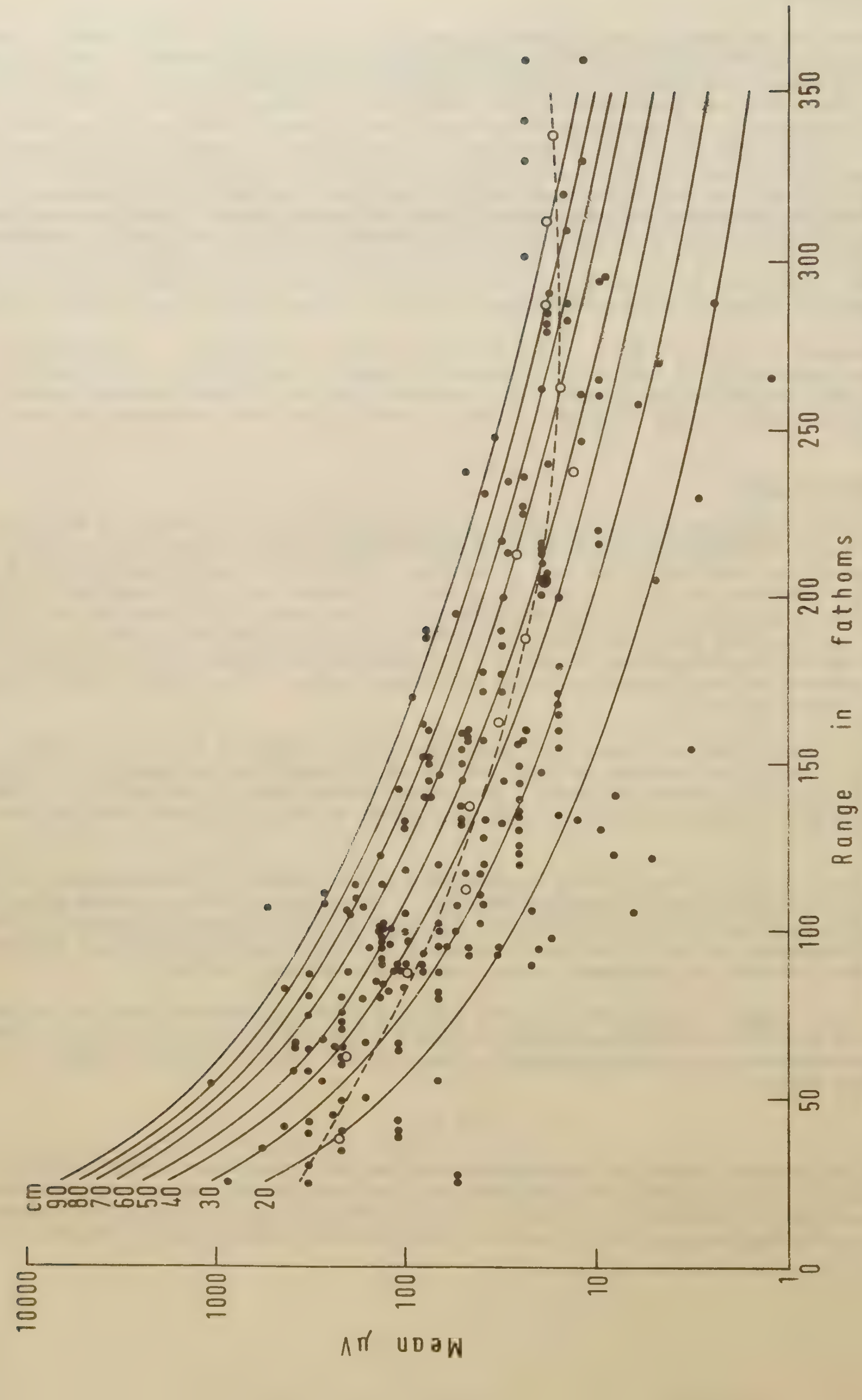

Fig. 1 Distribution of signal strength in µV for fish of lengths 20–90 cm for ranges up to 350 fm. The lines of signal strength in µV on range for different sizes of fish were derived from the measurements of Midttun and Hoff, (1962) and Cushing *et al.*, (1963). The observations of signal strength were made on hake off South Africa and S.W. Africa (Cushing, 1967b). The dashed line shows the mean signal observed on range, showing that bigger fish live in deeper water

2.1.3 Signal strength Signal strength in voltage can be measured at the peak amplitude, i.e. at minimum range. The best measure with present equipment is the average of such peak amplitudes, measured on a CRT. Such an average signal from a number of single fish in a range shell during a time period is given by $T.R^{-2}\delta_m$, where T is the target strength of the fish as at 1 m from the transducer, and δ_m is the directivity coefficient of the transducer at the mean angle, θ_m.

The signal strength of a single fish in range can be expressed in the sonar equation. There are two convenient formulations:-

$$E = T + S - 2H$$

where E is the echo level, S is the source level, T is the target strength, and H is the one-way propagation loss, including attenuation and spreading, all in db reference to 1 μ bar;

or

$$I_r = I_0 e^{-2ar}$$

where I_0 is the transmitted energy transmitted by the transducer, I_r is the energy received at the transducer, a is the attenuation coefficient, and r is the spreading coefficient, all in dynes/cm^2 (= 1 μbar). $T = I_0/I_r$; it is a dimensionless number, but it is convenient to refer it to a standard level of pressure or energy.

Figure 1 shows the relation of signal strength in μV ($T.R^{-2}.\delta_m$) on range, for series of fish sizes from 20 to 90 cm. The theoretical lines drawn on the figure are based on the measurements of Midttun and Hoff (1962), and Cushing et al. (1963), summarised in Cushing (1964). At extreme ranges, the signal of a single fish is detected only on the axis; i.e. $\delta_m \longrightarrow 1$ and $\theta \longrightarrow 0$. This effect is described in Cushing (1967a) and is taken into account in Fig. 1. The observations were made on hake off South Africa and S.W. Africa. Figure 2 shows the relation of signal strength in db ($T.R^{-2}$) on range in metres, this being given in logarithms (Nishimura 1963). The target strengths of tuna are taken from the work of Hashimoto and Maniwa (1956). The sound pressure is referred to the source level and the "reflection loss" is an estimate of target strength. The two forms of presentation in Fig. 1 and 2 have distinct applications. Figure 1 is helpful in using direct measurements from the CRT in μV at sea to make a quick appreciation of the average sizes of fish. Figure 2 is useful for any statistical analysis, being expressed in linear form.

A measure of relative target strength can be made from the average duration of signals from individual fishes in the beam (Cushing 1967a). Let $\bar{\alpha} = \frac{2R\sin\theta_m \cdot p}{V}$ transmissions or $\frac{2R\sin\theta_m}{V}$ sec, where $\bar{\alpha}$ is the mean duration of signal in transmissions or seconds, V is the ship's speed in m/sec, and p is the number of transmissions/sec. Therefore $\theta_m = \arcsin \frac{\bar{\alpha}V}{2R}$

Figure 3 shows the dependence of relative target strength on θ_m. So if an absolute measurement of target strength is made on a small number of traces, this technique can be used to employ all the information given on the paper record. It is assumed that the fish swim at zero speed or that their speed is a very small proportion of the ship's speed. In general fish do not swim on the same course as the ship.

In conclusion, there are a number of methods available to estimate the size of fish recorded as single fish traces. A combination of methods allows the full use of information to be made, so long as an estimate of average signal strength is made from a mean angle.

2.1.4 Numbers per unit volume Between any ranges, R_1 and R_2, the volume examined for a time period is given by

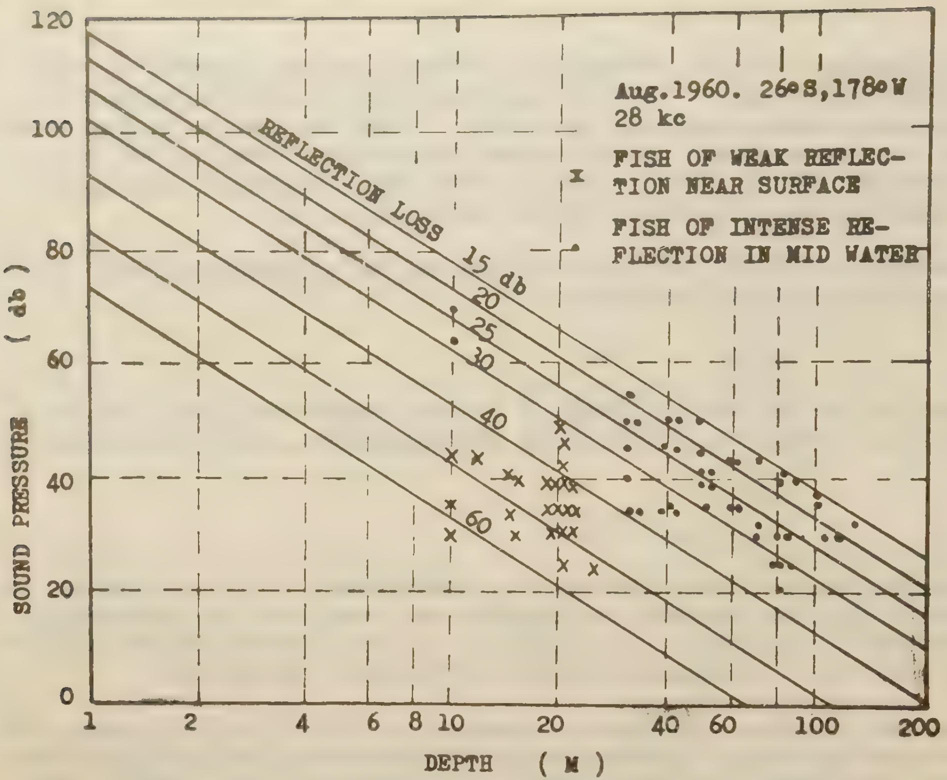

Fig. 2 Distribution of signal strength in db (reference the source level) for fish of lengths 20-90 cm on log depth (Nishimura, 1963); "reflection loss" is an estimate of target strength

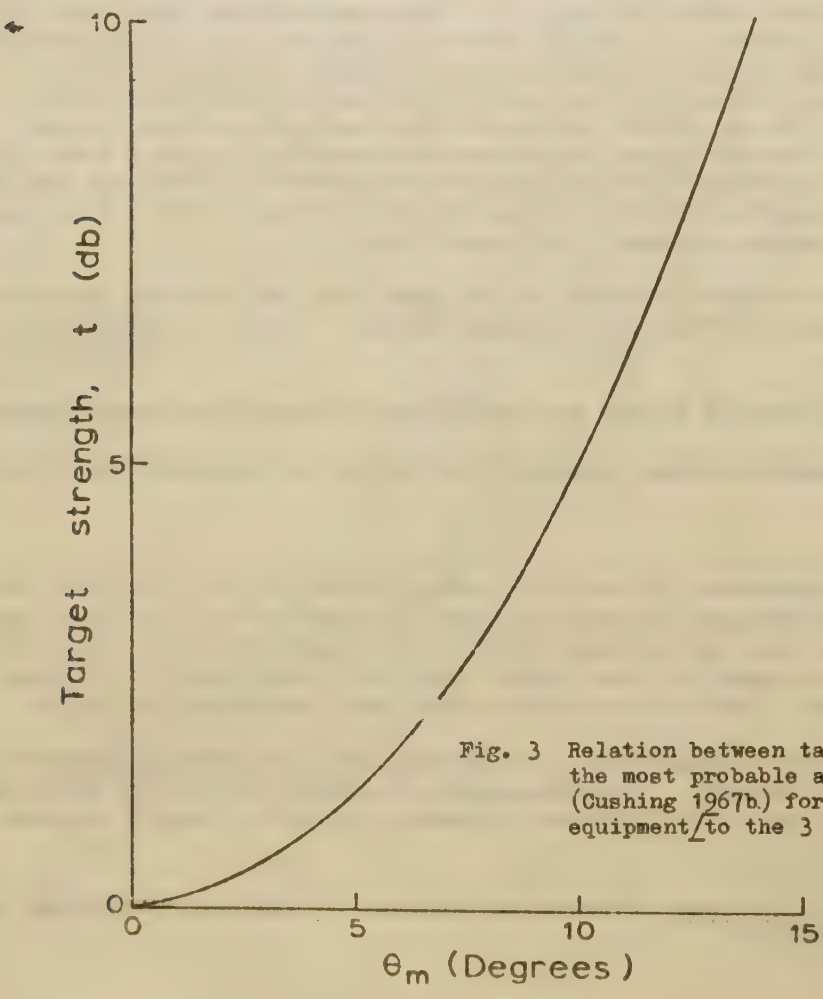

Fig. 3 Relation between target strength (T) and the most probable angle of detection (θ_m) (Cushing 1967b.) for the Lowestoft 100 kHz equipment [to the 3 db points, θ = 10°]

$$2/3\pi(R_2^3 - R_1^3)(1 - \cos \theta_{min}).$$

Similarly it is possible to calculate volumes in sectors of angle θ or range shell sectors. Each sector is weighted by the appropriate directivity coefficient, and the sum of the sectors is the effective volume sampled. This procedure takes into account the changes in directivity at extreme ranges, and estimates the chances of detection within the size ranges expected.

2.1.5 Summary For single fish traces, most of the desirable measurements (depth, signal strength, etc.) are indeterminate within rather wide limits. The disadvantage can be overcome by taking averages within a range sector and treating all observations as from the mean angle, θ_m. Then good estimates become available of true depth and signal strength, and hence of size of fish, duration of signal and numbers of fish per unit volume.

2.2 Shoals

There are two types of shoal trace, those much larger than the echo sounder beam and those much smaller. Those larger than the sound beam - layers, towers, steeples and mountainous traces - are probably correctly described in everything except vertical extent. Those smaller than the sound beam suffer from the disadvantages listed in the section on single fish. If they are hyperbolic traces, true depth and the number of shoals per unit volume can be estimated in the same way as for single fish. The vertical extent of the trace from the apex of the hyperbola is an estimate of shoal thickness, assuming a spherical shape.

The main difficulty in the representation of shoals on an echo chart is that an unknown part of the trace is composed of reverberation only. Figure 4 shows the trace of a herring shoal taken with a Lowestoft 100 kHz sounder (power output, 1 kW electrical power into the transducer; pulse length, 100 μsec; beam angle, 10° half angle to 3 db points). The inset shows a recording made at the same time with an MS 29 sounder (30 kHz; pulse length, $^1/2$ ms; power output, 1 kW electrical power into the transducer; beam angle, 25° half angle to 3 db points). The 100 kHz record shows two parts, an upper part differentiated perhaps into single fish, and a lower part, undifferentiated, which is presumably of reverberation. The 30 kHz trace does not show the separation into two parts, although it seems that the reverberation does not extend so far. Thus the vertical extent of an echo trace may not correspond to the vertical extent of a shoal in the sea.

3 ASPECTS OF FISH BEHAVIOUR AS OBSERVED WITH AN ECHO SOUNDER

3.1 Identification

By far the most important point about a fish trace is its identification, particularly as fish behaviour is the object of study. When the abundance of fish is estimated by echo survey, identification is made by commercial fleets or by research vessels working in the area, and the estimate of abundance is or should be limited to the depth zone in which the capturing gear is effective. An individual trace is never identified in this way, because it can be anything; the identification is really the extension of the chance of capture to the areas between points of capture. In a study of behaviour, the criteria become rather more critical. Traces must be identified rigorously and the best way of doing it is to go where the desired species is dominant to the point of excluding others. Examples are herring spawning grounds and cod spawning grounds.

Much work has been done on the deep scattering layer, the work of Hersey, Backus and Hellwig (1962) suggests that it is composed of fish, and Marshall (1951) has suggested that they are in the main myotophids. The layer migrates vertically towards the surface at night, and disperses or concentrates, roughly following certain isolumes, but it is unidentified by capture and therefore will not be examined further here.

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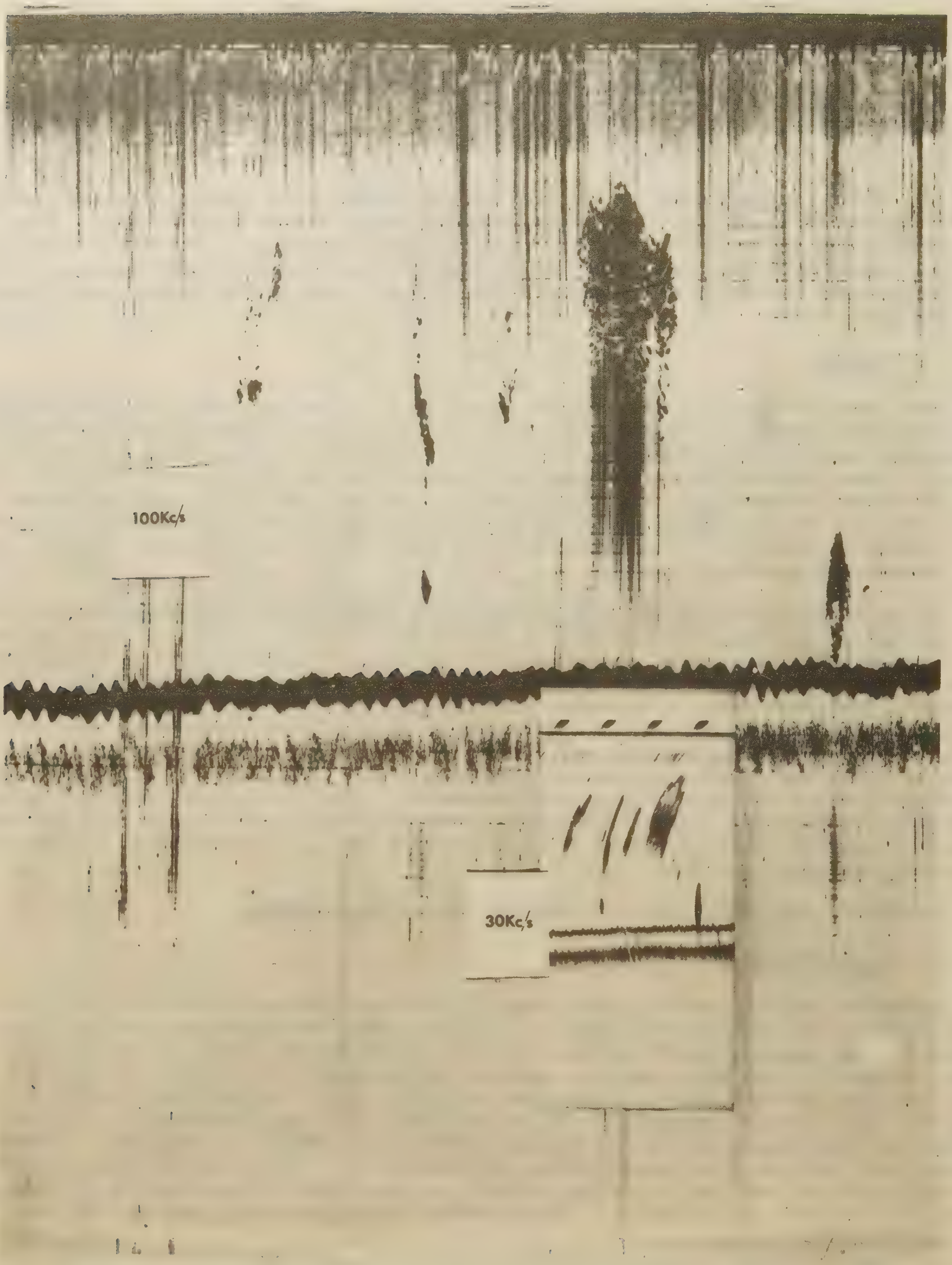

Fig. 4 Trace of herring recorded with the Lowestoft 100 kHz sounder and contrasted with the same recorded with an MS 29 30 kHz sounder. Note the reverberation shown with the high frequency machine

3.2 Diurnal variation in depth

The vertical migration of fishes from their day depths to the surface has been described by a number of authors. Richardson (1952) has described differences in herring migration off North Shields, Yorkshire, East Anglia and off Cap Gris Nez, all regions where herring predominated practically exclusively in the catches. He found a rough relation between the depth of shoal in the daytime and the Secchi disc reading; off Cap Gris Nez fish rose crom 75 ft at 1500 hr to 25 ft at 1700 hr, and by midnight they had returned to 40 ft. At Sandettié he noticed a "dawn rise" from 12.5 m at 0400 hr to 9 m at 0700 hr, after which they sank again to nearly 20 m by midday.

Furnestin (1953) has demonstrated a diurnal variation in depth for Sardina pilchardus on the purse-seine fishing grounds off Morocco. Brawn (1960) described a seasonal variation in the vertical migration of immature herring in Passamaquoddy Bay, confirmed by research vessel and commercial catches. She found that although the fish came towards the surface at night both in March and September, the seasonal variation in day depth was not related to seasonal variation in radiation.

Haram (1965) has shown a diurnal variation in the depth of two layers of single fish in Lake Bala (N. Wales). The upper layer was composed of roach and the lower of gwyniad (whitefish; Coregonus spp). Northcote (1964) described a vertical migration of Chaoborus (larval insects with air bladders) in a Canadian lake. Johnson (1961) showed that sockeye salmon (Onchorhynchus nerka) live between 0 m and 3 m in daylight, that they rise to the surface at dusk, disperse downwards as far as 15 m in full darkness, and then rise back to the surface at dawn. He also showed how the salmon gathered at one end of the lake under stress of the prevailing wind. In principle, from the more detailed work of Richardson (1952) and Johnson (1961), it appears that fish live at a day depth determined by the light intensity, rise to the surface at dusk, disperse or sink after midnight, and rise again to the surface at dawn. The general pattern of vertical migration resembles that for planktonic crustacea elucidated in Cushing (1951).

A number of papers have been referred to by Woodhead (1965) as showing a vertical migration of cod. He was interested in the diurnal variation of cod catches with a trawl. His echo charts show differences in distribution but there is no evidence of identification in the layers above the bottom.

3.3 The effect of artificial light

Richardson (1952) showed that when an underwater light was switched on in darkness, herring appeared to dive and then slowly adapted themselves to their previous depth, when the light was switched off. In fishing off Cornwall, however, pilchards were found to be attracted by light. Blaxter and Parrish (1958) showed that whiting, herring and sprats tended to aggregate beneath lights at night. Whiting aggregated at about 0.1 lux, whereas herring and sprats aggregated at 1,000 to 10,000 lux. This is the type of experiment that can be made at sea with lights, an echo sounder and identifiable fish shoals, to confirm the application of physiological rules determined in the laboratory.

3.4 Densities of fish

Individual fish traces have been recorded from tuna in various parts of the Pacific. The methods are not exactly those described above but resemble them closely; the differences in density observed are very large. They are:-

"tuna"	Daito Shima	$9.1.10^{-7}/m^3$
	Luzon Is	$27.8\text{-}10^{-7}/m^3$
	S. Pacific	$1.0.10^{-4}/m^3$
	Tsuguru	$2.0.10^{-4}/m^3$ (Shibata 1962, 1965)
albacore	New Zealand	$30.0.10^{-5}/m^3$
yellowfin	New Zealand	$0.1\text{-}90.0.10^{-5}/m^3$
bluefin	New Zealand	$200.0.10^{-5}/m^3$
big eye and yellowfin	New Zealand	$2.0\text{-}16.0.10^{-5}/m^3$ (Nishimura 1961)

Very roughly, the observations range from $1.10^{-4}/m^3$ to $1.10^{-6}/m^3$, a range of one hundred times.

A different form of estimate was made by Cushing (1957) by taking ratios of the pilchard stock in numbers to quantity of echo trace over a period of five months throughout the area of the English Channel. There were 6834 pilchards/transmission, or $1.96/m^3$, a very rough estimate because although pilchards were dominant a minority of other fish were present. Further, the estimate of the volume sampled is a very rough one.

To estimate fish density, Truskanov and Scherbino (1965) have used underwater cameras and underwater transducers in fish shoals, together with estimates of voltage received from shoals (assuming that $v = k\sqrt{n}$, where v is the voltage received from a fish shoal, n is the number of fish in the shoal, and k is a constant). These authors estimate the density of Atlanto-Scandian herring in the Norwegian Sea to be $0.68\text{-}1.0/m^3$. The density of cod in the Barents Sea was $0.12\text{-}0.78.10^{-4}/m^3$. The observations may be summarised as follows:

		Density (n/m^3)	Distance between fish (m)
pilchard	(20 cm)	2.0	0.79
herring	(30 cm)	0.7-1.0	1.00
cod	(70 cm)	$1.0\text{-}8.0.10^{-5}$	43.8-90.9
tuna	(100 cm)	$1.0.10^{-4}\text{-}1.0.10^{-6}$	22.2-100.0

There are not enough data to determine the dependence of density on size of fish. There is a range of three to five times in size, but a range of more than a million times in density or a hundred times in distance apart. A larger number of observations would determine the nature of the relation.

3.5 Speeds of fish

Haram (1965) has compared the differences in the length of trace of gwyniad (*Coregonus* spp) at the same depth by night and day in Lake Bala. During daylight the fish swam five to ten times faster than at night, but no absolute estimate could be made. Shibata (1962, 1965) has made estimates of the speeds of tuna crossing the echo sounder beam; they range from 0.05 kn to 15.0 kn, but mostly about 1 to 4 kn. The measurements allow for different sizes of fish (estimated from measurements of target strength), but not for the distribution of targets in the beam about the mean angle, θ_m. Hence the sizes of fish were underestimated.

Kawada and Tawara (1958) devised a method of estimating the speed of yellowtails swimming into and away from a set net. A transducer was set at the mouth of the net firing downwards along the track of entry and exit. The speed can be determined so long as the fish swim in the same direction as the axis of transmission. These authors estimate that the fish were swimming at 0.01-0.03 m/sec.

3.6 Shapes of shoals

Belloc (1935) watched sardine shoals near the surface from a balloon and found that they were shaped like veins along the tide. Bolster (1958) found the same pattern for herring shoals in the Sandettié area. He charted the area of large spawning shoals of herring and found that they lay with their long axes along the tidal streams. Aoyama (1960) charted the horizontal distribution of three large shoals of hairtail in the East China Sea. The shoals were 4.0-5.5 miles long and 3.0-4.0 miles across. They were 10 m deep and the average distance between the shoals was 5 miles.

Large shoals can be readily charted in this way. Truskanov and Scherbino (1966) have charted shoals of Atlanto-Scandian herring in the Norwegian Sea and at the same time estimated the density by the methods noted above. Echo sounders on research ships can be used to describe the very large shoals of fish that are sometimes found; it will be shown below that scanners can examine small shoals, and describe their shape and density.

4 INFORMATION GIVEN BY A SCANNER

A scanner insonifies roughly the same volume as an echo sounder, but it has a very high angular resolution. Hence the statistical approach used for the echo sounder is not necessary to overcome the indeterminacy of estimates referred to above. The beam is 30° in horizontal spread and 10° in vertical spread. The angular resolution is 1/3 of a degree and the range resolution is 100 μsec. This means that the unit of scanning in plan is less than a foot wide and about three inches long, but it is 10° in depth. Hence although single fish arrayed at one depth can perhaps always be resolved, the signals in depth within the unit of scanning can become superimposed.

The information is presented on a B-scan, bearing on range, distorting the true polar co-ordinates to some extent. If the transducer is fired horizontally, information is presented as if in plan. Scanning is complete within the transmission of the pulse of sound and so there is a rapid repetition of the complete plan, perhaps four times per second. The plan of the scan can show the horizontal shapes, their sizes, and their changes in time. Further, the scanned shoals are resolved into small units which are often single fish but which need not be. However, in firing horizontally, the scanner, like all sonars, must suffer from the refractions due to layering in the sea and to variations in aspect of the targets. Hence estimates of target strength may become very variable indeed under some conditions.

The scanner can be fired vertically downwards and then it yields information on the vertical distribution of fish and on the shapes and sizes of shoals in vertical transect. In this mode, it might become possible to estimate target strengths. Individual signals within the same shoal have been counted on many successive frames (Cushing and Harden Jones, 1966). Gulland (in an appendix to Cushing and Harden Jones, 1966) has pointed out that the chance of a single fish occurring in the unit of scanning follows a Poisson distribution. Hence the plot of numbers of individuals on range can be extrapolated to zero range (where only individuals can occupy the unit of scanning) to give a true estimate of numbers.

Fired vertically, the scanner also gives a correct picture of the vertical distribution of fish just above the sea bed. Fired obliquely, this information is still

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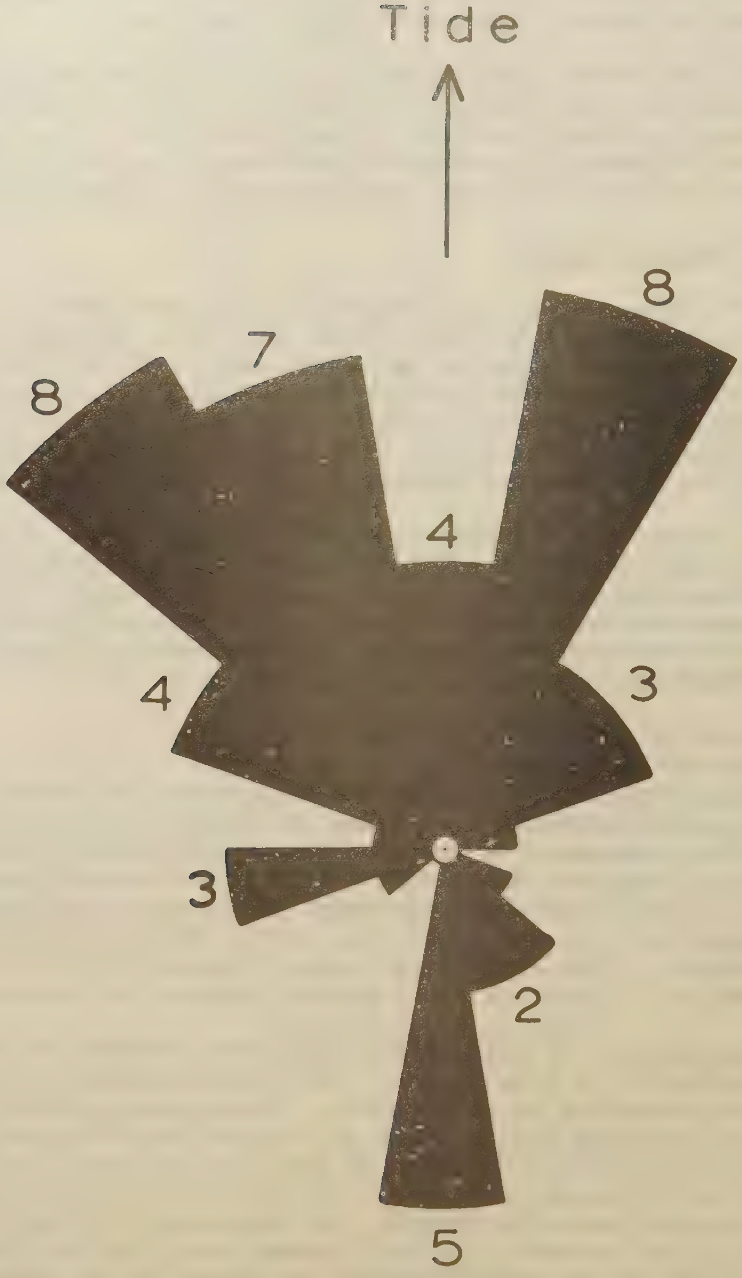
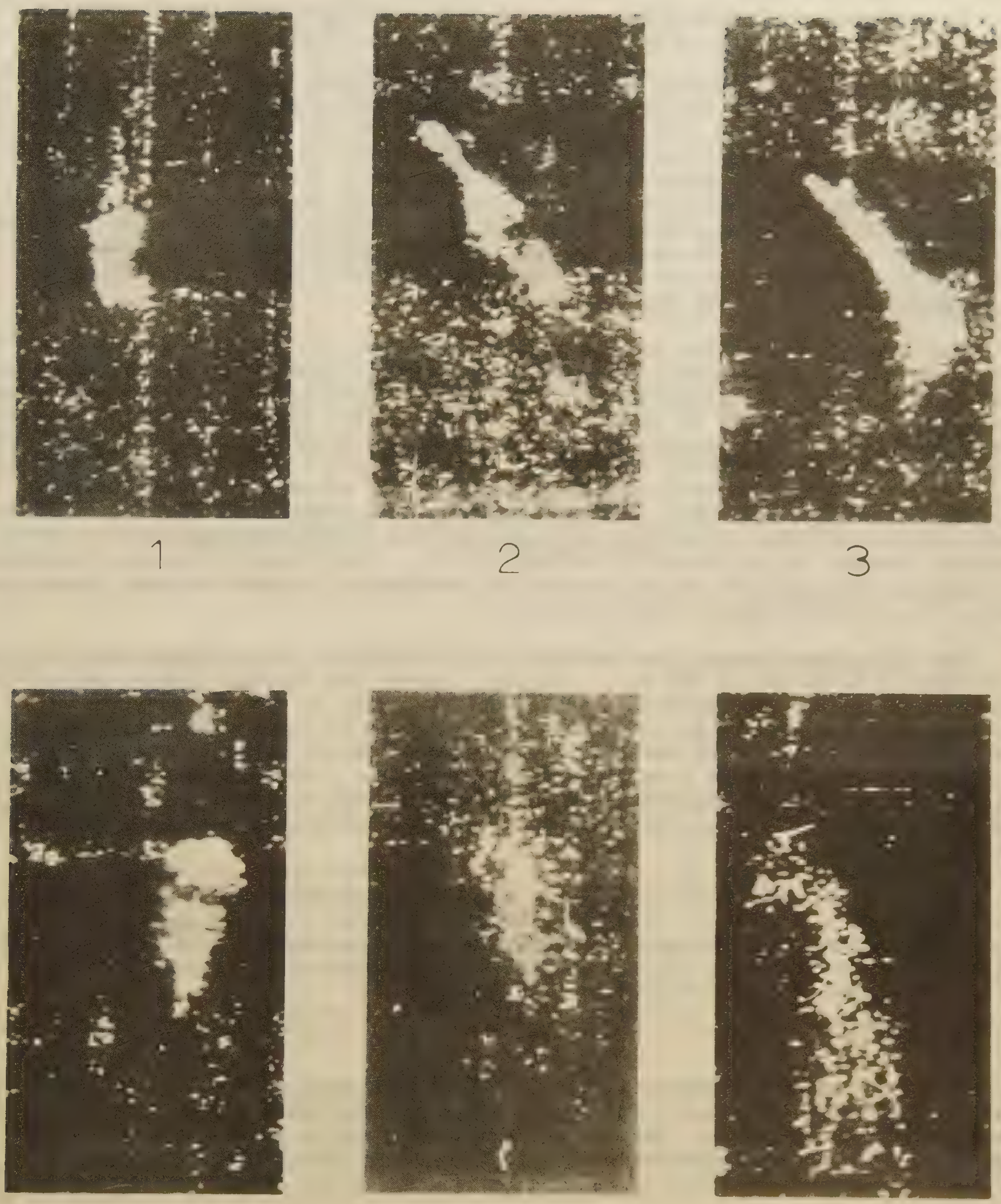


Fig. 5 Polar distribution of movements of herring shoals with respect to the tidal streams (Harden Jones and McCartney 1962)



1 2 3

4 5 6

Fig. 6 Shoal patterns observed with the bifocal equipment (Cushing and Harden Jones 1966)

given correctly; however, its precision may be vitiated by rocks, boulders and other roughnesses.

5 ASPECTS OF FISH BEHAVIOUR AS OBSERVED WITH A SCANNER

Sector scanners have not yet been used sufficiently to explore all aspects of fish behaviour. This section is concerned only with some points that have arisen.

The first use of a sector scanner to study fish behaviour was by Harden Jones and McCartney (1962). They observed the movement of herring shoals in the southern North Sea past an anchored ship, with a sector scanner. At the same time they observed the current flow. They found that the herring shoals were in the main drifting with the tide. Fig. 5 shows the polar distribution of movement with respect to the tide. This confirms observations made by Harden Jones (1962), tracking herring shoals with an echo sounder and a Decca track plotter in the southern North Sea. Similar observations for pilchards by Harden Jones are given in Cushing and Harden Jones (1966). They are very important observations because they suggest that fish drift with the tide or current rather than stem the tide or current.

The obvious information on shoals is that on size and shape. Figure 6 shows a number of shoals observed with the bifocal equipment firing horizontally and hence in plan view. It will be readily seen that there is a variety of shapes, some of them unexpected, and a variety of densities. The shapes and densities were maintained for many frames. There is not yet enough information to elicit any rules on shoal formation. In Cushing and Harden Jones (1966, Fig. 5) a set of remarkable pictures is given of two ribbon-like shoals, each with outriders, swimming independently but turning to meet and fuse when they come within visual range of each other. In the same publication (Fig. 12) a fish is shown for many frames swimming at a position half-way between the two doors of an Engel trawl. Both observations are remarkable, but indicate the capacity of the scanner in observation, rather than any fundamental advance in our knowledge of fish behaviour.

The Birmingham scanner has been used in a variety of experimental studies on fish behaviour in tanks and in the sea. Welsby, Blaxter and Chapman (1963), showed that herring and dogfish were herded across a tank by a rope or net, in daylight or in darkness but that the herding process was more pronounced in daytime. Welsby et al.,(1964) contrasted the behaviour of herring in tanks and at sea in light and in darkness, showing that the fish were more dispersed in darkness. This can be shown with an echo sounder. But the observation is more precise with a scanner because the distance apart of individual fish can be estimated, whereas with the sounder only the average distance can be measured.

Cushing and Harden Jones (1966) also show that a midwater trawl can be very clearly delineated with a scanner. Fish were observed swimming in along one wing, across the square and out by the other wing. They were also shown swimming at points along the cables. The point really is that the great capacity in observation can be used to determine what fish do when in contact with gear.

6 DISCUSSION

The study of fish behaviour requires exact laboratory experiments coupled with extensive observations at sea. Because fish species obviously differ markedly in their behavioural characteristics, their identification needs to be rigorous. With an echo sounder it is possible to estimate the size of a fish, but not its identity. Therefore any behavioural observations should be limited to the depth zone in which capture is valid.

The observations at sea with an echo sounder were listed under diurnal variation (and experiments with lights), densities and speeds of individuals, and shapes of shoal. Analogous observations can be made with a sector scanner. Both instruments deceive to some extent. A firm knowledge of the statistical basis of echo sounding observation is needed to extract the most information in an unbiased way. The sector scanner information should often be transformed to polar co-ordinates to get the best use of information.

The type of information that can be properly obtained, on densities of individuals, shoal packing and shapes, swimming speeds, etc. is the sort of information that can be readily linked with laboratory measurements of speed, perceptive range and space requirements. It is only then that the acoustic instruments will find their full use in the study of fish behaviour.

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COMPARATIVE AND EXPERIMENTAL FISHING AS METHODS FOR STUDYING FISH BEHAVIOUR IN THE NATURAL ENVIRONMENT

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Abstract

Advantages and limitations of both comparative and experimental fishing as methods for studying fish behaviour are discussed. It is emphasized that these methods are limited largely to determining what changes occur in catch composition as a result of gear modification, and that other techniques are usually necessary for establishing why they occur.

VALEUR DE LA PECHE COMPARATIVE ET DE LA PECHE EXPERIMENTALE COMME METHODES D'ETUDE DU COMPORTEMENT DU POISSON DANS LE MILIEU NATUREL

Résumé

L'auteur examine les avantages et les limitations de la pêche comparative et de la pêche expérimentale en tant que moyens d'étudier le comportement du poisson. Il souligne que d'une manière générale ces méthodes permettent seulement de constater l'évolution de la composition des prises à la suite de modifications apportées aux engins de pêche, et qu'il faut d'ordinaire avoir recours à d'autres techniques pour connaître les raisons de cette évolution.

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LA PESCA COMPARATIVA Y EXPERIMENTAL PARA ESTUDIAR EL COMPORTAMIENTO DE LOS PECES EN EL AMBIENTE NATURAL

Extracto

Se describen las ventajas e inconvenientes de la pesca comparativa y experimental en el estudio del comportamiento de los peces. Se indica que estos métodos de estudio se limitan principalmente a determinar qué cambios ocurren en la composición de las capturas como resultado de las modificaciones del equipo, y que generalmente se necesitan otras técnicas para determinar por qué ocurren.

1 INTRODUCTION

Ideally, a fishing gear should catch fish without their being aware that they are caught and have no escape (e.g. lines, purse seine), or despite their attempts to escape (e.g. fast trawls, mullet seines), or by utilizing their natural escape reaction to ensure their capture (e.g. Danish seine, bag nets).

Mostly, fishing gear has evolved over the centuries in such a way as to produce effective gears for the capture of particular species in particular environments under particular conditions. At each stage in evolution the criterion has been simply whether any change in gear made it more efficient simply in catching. Such knowledge of fish behaviour as existed was sometimes used, albeit unwittingly, for improvement of gear. The use of fishing as a means of studying fish behaviour has been very limited, and for good reason.

This review is restricted to the use, for studying fish behaviour, of plain fishing gear without the assistance of any instrumentation. In such studies, all conclusions must be drawn only from a combination of observation of catches made, knowledge of mechanical and geometrical features of the gear used, and knowledge of the exact conditions under which the gear was operated, e.g. water movements, visibility, etc.

2 EXPERIMENTAL FISHING

The evolution of fishing gear may be considered as a long and protracted series of experimental fishings. In these, alterations have been made to the gear and, after extensive fishing experience, they have been shown to have resulted perhaps in improved catches, in which case they have been permanently adopted, or in poorer catches, in which case they have been abandoned, or in not appreciable changes in catches, in which case their fate depended upon such factors as whether they represented a simplification in fishing technique which was itself worthwhile when other things were equal.

Experimental fishing tells us only that a particular gear either does or does not catch more than another gear; the reasons why have to be surmised. Straightforward experimental fishing (i.e. trying-out) either of a new gear in an established fishery or of established gear in a projected new fishery does not provide any direct evidence of exactly how the fish behave in relation to the gear, but only indicates that the gear being used either does or does not match the behaviour of the fish in such a way that the fish does or does not get caught. The detailed investigation of fish behaviour in relation to gear requires a combination of experimental fishing and suitable instrumentation of the types considered by Dr. Cushing and Dr. Mohr in their reviews of methods at this conference.

3 COMPARATIVE FISHING

True comparative fishing involves alternate and repeated fishings, or parallel side by side fishings, arranged in such a way that, after a series which must be extensive enough, conclusions can be drawn with certainty, borne out by statistical analysis, that one method or gear is or is not better than another or that differences in catches are due entirely to one variation of gear, all else being equal. The technique can be extended to measure the difference in catching effectiveness between gears, but accurate measurement of this will usually involve a very long series of fishings indeed.

A series of comparative fishing experiments can be so arranged that, by combining the results of each experiment designed to show the effect on catches of just one variation in gear, a picture of how fish are caught may be built up.

4 PUBLISHED RESULTS

Mohr (1960) fully reviewed the subject of fish behaviour in relation to fishing gear; he and Aslanova (1958) drew attention to what few findings on fish behaviour had come from fishing experiments; their bibliographies were extensive. Much of the bibliography attached, which refers only to papers drawing conclusions about fish behaviour from fishing experience, was drawn from the reviews of Mohr and Aslanova. In many of the works the conclusions from actual fishing experiments were only incidental. Mohr made the very important point " .... a complex of stimuli always emanates from fishing gear, and it is, in fact almost impossible to consider individual components in isolation .. and therefore, in the case of field observations, assertions regarding the causality of reactions should by no means always be accepted without reservation".

That fish see nets of certain colours and avoid swimming into them is a fairly safe conclusion from fishing trials with gillnets, especially when different coloured nets have been fished together (Tokarew 1958, Aslanova 1958, Meseck 1928, Baranov 1939, Koike 1958, von Brandt 1953, Schwarz 1958 and 1959, and Kajewski 1958). The conclusion that sardines became meshed in the forward netting of a trawl because they did not see it in dirty water (Gulbadamov 1958) is reasonable but less reliable, because a moving trawl confronts fish with a complexity of stimuli. The evidence from fishing is that fish see air-bubble screens and keep away from them (Anon. 1958 and Anon. 1959). Bagenal (1958) designed and carried out an experiment to measure the effect of fitting bridles to a trawl; he discounted the visual effect of bridles and suggested that their vibrations were most important. Bridger (1967) from results of parallel comparative fishing experiments developed a hypothesis that demersal fish see, or are aware of, parts of trawling gear in advance of the net, that they swim away from them, and that the disturbed fish excite others. His data so far only suggest that this might be so and much more experimental data are required to fully test the hypothesis. This is a good example of how time-consuming and ponderous the method of comparative fishing is for elucidating fish behaviour - a job for which Bridger's original experiments were not planned - although it is ultimately the only way of finding out whether one gear catches more than another.

Imamura and Ogura (1957) because they found an optimum trawling speed for biggest catches, deduced that, demersal fish were able to swim away from the trawl at low speed and were warned of its advance by a pressure field at higher speeds. That small fish actively escape from the codend of a trawl while it is being towed was shown by Davis (1934). Todd (1911) and Margetts (1963) showed that different species of demersal fish probably reacted differently when they encountered various parts of a trawl net, but neither author attempted to conclude what was the exact pattern of behaviour of fish in the net. Parrish (1951) suggested that differences between trawl catches were partially due to some fish being active enough to escape when scared by turbulence caused by one of the gears and not by the other, and Zupanovic and Grubisic (1958) suggested that the use of one sort of trawl bridle caught more of the bigger and faster-swimming fish because of their liveliness, and that differences in catches were due to differences between species in their behaviour in relation to the different sorts of bridles. Both of these conclusions are, at best, very contentious, because of the complexity of the stimulation and uncertainty about the exact nature of any fish reaction which affected whether the fish escaped or was caught. Kennedy (1951) thought that the decrease in catching efficiency of a gillnet with saturation might be due to the fish-scaring effect of the turbulence caused by the fish already caught.

Von Brandt (1940, 1941 and 1949) suggested that the avoidance reaction of fish was influenced by the feel of the material of the net, and Predel (1959) also put this forward as an explanation of variation in catches, but the point is certainly arguable, with different visibilities and different net mechanics also being likely contributory causes.

From fishing observations, conclusions about the reactions of fish to noise have been confined merely to whether or not fish are scared. Aslanova (1958), Schärfe

(1959), Dragesund (1958) and Margetts (1967) all refer to the apparent scaring of pelagic fish by noise of gear or ship, although Schärfe (1956) and Strasburg and Yuen (1958) claimed respectively that Gadoids and tuna were not disturbed by noise. These observations were mostly made directly or with instruments in conjunction with catching success, so that their inclusion here as findings from experimental fishing is not strictly correct.

The avoidance by eels of pots with distasteful odours (von Brandt 1956) is a clear example of a behavioural response to one particular stimulus which a gear presents, whereas the suggested smell-reaction of lobsters (von Brandt 1959) is still unproven.

From angling results and examination of the stomachs of tuna caught, Hotta, Kariya and Ogawa (1959) deduced that hungry fish stimulated even those with full stomachs to snap at hooks. Von Brandt (1954) explained some of the differences in success of fishing for herring with coarse and fine gillnets in the North Sea and the Baltic in terms of differences between the behaviour of fish in big and in small schools.

Woodhead (1964 and 1965) drew conclusions from trawl catch results about the diurnal behaviour of demersal fish, as features of their biology rather than their reaction to fishing gear; he tended to ignore the likelihood of their reaction to the gear changing diurnally, as indeed was shown to happen by Mohr (1963). Often, in commercial fishing, tactics and gear are or have been adapted to known or suspected diurnal changes in fish distribution and behaviour.

Occasionally some fishing results have been explained as showing that bigger fish swim further and faster than smaller ones (Bridger 1967, Margetts 1949a,b, Zupanovic and Grubisic 1958) but although these conclusions may be correct, comparative fishing is not a practical way of making reliable and accurate observations of fish swimming speeds. Creutzberg (1961) used net catches, when the tide was flowing in different directions, to show how elvers moved in relation to water currents; such fine distinctions as he was showing require a most precise knowledge of the relative speeds of fish, water, and net, which cannot always be obtained.

5 REMARKS

Comparative fishing and experimental fishing are, by themselves, poor means of investigating fish behaviour, although deductions about fish behaviour have frequently been made to help explain the results of such fishings. They can provide pointers to the fish reaction to the gears, but to be really useful in this field they must be accompanied by accurate measurements of all relevant conditions such as water flow, illumination, sound, etc. Comparative fishing must be the ultimate test of the effectiveness of any gear, but such fishing is directed to showing what the gear catches; how it catches fish is best investigated by other means and experiments. Comparative and experimental fishing are not well suited to show, from catches, how fish behave, but are frequently useful, the other way round, to show how catches are affected when gear has been modified or designed so that known fish reactions to gear are made use of or countered in an attempt to aid the catching process.

The crudeness of comparative fishing as a research tool is well known to those who have used it, and has been indicated in statistical terms by Gulland (1967), who described its limitations of accuracy and showed how very long some series of comparative fishings must be to give a reliable answer to a simple question on catching effectiveness.

In general, it will be best to use experimental fishing and comparative fishing just for their real purpose of finding out the effect of gear or parts of it on catches, and while doing so to investigate and accurately describe the gear in terms of the stimuli it presents to fishes. It should also be rewarding to make a thorough study of established commercial fisheries and deduce why it is that certain gears work better than others in particular fisheries. The final conclusions as to how fish sense gear, and how and why they react to it, are better left to instrumental fishing and controlled experiments avoiding the many uncontrollable variables that affect the limited type of comparative fishing and experimental fishing experiments considered here.

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A REVIEW PAPER ON THE BEHAVIOUR OF FLATFISHES

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Abstract

Data are given concerning the behaviour of both commercial and non-commercial species of flatfish. Behaviour characteristics are reviewed and discussed under various categories including feeding habits, diel activity, nature and method of locomotion, vertical migration, spawning, and response to various stimuli.

ETUDE SUR LE COMPORTEMENT DES POISSONS PLATS

Résumé

L'auteur fournit des données touchant le comportement de diverses espèces de poissons plats, exploitées ou non par la pêche commerciale. Les caractéristiques de comportement sont examinées sous diverses rubriques : habitudes alimentaires, activité nycthémérale, type et mode de locomotion, migrations verticales, reproduction, et réactions à divers stimuli.

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DATOS SOBRE EL COMPORTAMIENTO DE PECES PLANOS

Extracto

El autor da datos relativos al comportamiento de especies comerciales y no comerciales de peces planos. Reseña las características del comportamiento y las examina en varias secciones que comprenden hábitos alimentarios, naturaleza y métodos de locomoción, migraciones verticales, desoves y reacción ante diversos estímulos.

1 INTRODUCTION

The paper presents data concerning the behaviour of flatfishes (Pleuronectiformes) in relation to fisheries. This is done in the widest sense, although primarily directed towards fisheries research. To get a better insight into the behaviour of flatfishes it is necessary also to review the work done in the field of physiology. An attempt will be made to demonstrate the main outlines of behaviour, therefore non-commercial species are also included. Useful for the study of behaviour are some monographs on commercial species, sometimes not covering the strict field of behaviour, but undeniably of interest for a better understanding of the behaviour. These include: Plaice-Cole and Johnstone (1901) and Wimpenny (1953); Starry flounder-Orcutt (1950); Lemon sole - Rae (1965); Common sole - Cunningham (1890). Where possible, the British common name of a species has been used; in other cases the English common name.

2 FEEDING

2.1 Field observations on stomach contents

Data on the composition of the food in the stomach of flatfishes are given in Table I. The food animals are arranged in phyla and the frequency of occurrence in the stomachs of the different phyla is noted according to point method, 1 for the most important, and so on to 5 in decreasing importance. By means of this point method a division could be made according to the feeding habits: I-Polychaeta-Mollusca feeders, II-Crustacea feeders, III-Fish feeders. The Table shows the composition of the food found in the stomachs of juveniles and adults only. Larval and post-larval stages are not incorporated. The most important conclusion which can be drawn from the Table is that as a rule Bothidae feed on fish or on other quick moving animals, such as shrimps. The Soleidae are Polychaeta-Mollusca feeders. The Pleuronectidae take up a position in-between, we find genuine fish feeders like the halibut (*Hippoglossus hippoglossus*) and pure Crustacea feeders like the starry flounder (*Platichthys stellatus*) but also Polychaeta-Mollusca feeders such as the lemon sole (*Microstomus kitt*). Variations in the diet can be explained in terms of regional and local differences in the invertebrate fauna. The feeding condition is also a very important factor, for a hungry fish will be less selective than a well fed fish. In the flatfish group (*Pleuronectiformes*) we generally observe a shift in the diet with increasing age, from smaller to larger food animals and from more or less immobile to more agile food. Food habits have been reported by: Franz (1910), Huntsman (1918), McIntyre (1953), Nikolaev (1955), Pearcy (1962) and Redeke (1909).

2.2 Experimental work

On digestion in fish a great deal has been done: Bayliss (1935), Bückmann (1952) and Dawes (1930a,b,c). Histo-morphological work has been carried out by Dawes (1929),Koltzer (1956), Ochiai (1966), Pilliet (1893 and 1894), and Suyehiro (1941), but their studies have no direct bearing on the study of fish behaviour. Of more importance is the digestion rate which was reported by Karpewitsch and Bokowa (in Buddenbrock 1956) and Dawes (1930a,b,c). Both give for flounder (*Pleuronectes flesus*) 48-60 h, and for plaice (*Pleuronectes platessa*) 54-60 h. These values however do not tally with what has been found in the field. Arndt and Nehls (1964) found for young flounders 14-16 h; Franz (1910), De Groot (1964) and Petersen (1911) found that the stomachs of plaice were nearly empty in the early morning. From these observations we may conclude that food leaves the intestinal tract in flounder and plaice within 24 h. Hatanaka *et al*. (1954) made a division according to morphological features, such as the relation between maxillary length and body length, gill-raker and intestinal loop, which agrees with the feeding habits. He made use of the following species: *Eopsetta grigorjewi*; *Kareius bicoloratus*; Japanese dab, *Limanda herzensteini*; Yokohama dab, *Limanda yokohamae*; Slime flounder, *Microstomus achne*; frog flounder, *Pleuronichthys cornutus*; bastard halibut, *Paralichthys olivaceus*.

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TABLE 1. OCCURRENCE OF FOOD ANIMALS IN FLAT FISH

Groups: I Polychaeta - Mollusca feeders. II Crustacea feeders. III Fish feeders

Scientific Name	Common Name	Area
BOTHIDAE		
Arnoglossus laterna	scald-fish	North Sea
Caulopsetta scaphus	New Zealand megrim	Pacific (N.Z.)
Colistium guntheri	New Zealand brill	Pacific (N.Z.)
Colistium nudipinnis	New Zealand turbot	Pacific (N.Z.)
Lepidorhombus whiffiagonis	megrim	North Sea ....
	megrim juv.	North Sea
	ad.	North Sea
		North Sea
Paralichthys olivaceus	bastard halibut	Pacific (Japan)
Paralichthys dentatus	summer flounder	Atlantic (USA).................
Paralichthys oblongus	fourspotted flounder	Atlantic (USA)
Paralichthys olivaceus	bastard halibut	Pacific (Japan)
Scophthalmus maximus	brill	North Sea
		North Sea
		North Sea ....
		North Sea
Scophthalmus rhombus	turbot	Baltic
		North Sea
		North Sea
		North Sea ....
Scophthalmus norvegicus	Norway topknot	North Sea
Scophthalmus maximus	brill	North Sea
Scophthalmus rhombus	turbot	North Sea
PLEURONECTIDAE		
Eopsetta grigorjewi	roundnose flounder	Pacific (Japan)...............
Eopsetta jordani	petrale sole	Pacific (USA)
Hippoglossoides elassodon	Japanese halibut	Pacific (Japan)
Hippoglossoides platessoides	long rough dab	Atlantic (Canada)
Hippoglossus hippoglossus	halibut	North Sea
		Atlantic (UK) ....
Hippoglossus hippoglossus	halibut	Atlantic (USA)
Hippoglossoides platessoides	long rough dab	Atlantic (USA)
Kareius bicoloratus	-	Pacific (Japan)
Lepidopsetta mochigarei	Japanese plaice	Pacific (Japan)
Limanda ferruginea	yellowtail	Atlantic (USA) ....
Limanda herzensteini	Japanese dab	Pacific (Japan)
Limanda limanda	dab	North Sea
		North Sea
		North Sea
		Baltic ....
		North Sea
		North Sea
		White Sea
		North Sea
Limanda limanda	dab	North Sea.....................
	dab juv.	Atlantic (Iceland)
	dab	North Sea
Limanda yokohamae	yokohama dab	Pacific (Japan)
Microstomus achne	slime flounder	
Microstomus kitt	lemon sole	North Sea
		North Sea ....
		North Sea

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Food types: P - Polychaeta L - Coelenterata E - Echinodermata F - Fish
M - Mollusca A - Ascidae C - Crustacea

	Group	P	M	L	A	E	C	F	Reference
	II						1	2	Steven, 1930
	III						2	1	Graham, 1965
	III						2	1	Graham, 1956
	II						1		Graham, 1956
....	III							1	Fulton, 1905
	II		3				1	2	Rae, 1963
	III		3				2	1	Rae, 1963
	III							1	Steven, 1930
	III						2	1	Hatanaka, 1954
....	III	4	3				2	1	Bigelow, 1953
	III	4	3				2	1	Bigelow, 1953
	III						2	1	Kosaka, 1966
	III							1	Franz, 1910
	III							1	Fulton, 1905
....	III						2	1	Hartley, 1940
	III							1	Steven, 1930
	III							1	Hertling, 1928
	III							1	Holt, 1895
	III							1	Franz, 1910
....	III							1	Rae, 1957
	II						1	2	Steven, 1930
	III							1	Redeke, 1906
	III	4	3				2	1	Redeke, 1906
....	II						1	2	Hatanaka, 1954
	II						1	2	Ketcher, 1966
	II						1		Suyehiro, 1934
	II		2				1		Huntsman, 1918
	III		2					1	Joensen, 1954
....	III						2	1	McIntyre, 1953
	III		3				2	1	Bigelow, 1953
	II	4	3			1	2		Bigelow, 1953
	I	1	3				2		Hatanaka, 1954
	I	1					2		Suyehiro, 1934
....	II	3	2				1		Bigelow, 1953
	I	1					2	3	Hatanaka, 1954
	I	2	1				3		Blegvad, 1916
	II	3	4			2	1	5	Fulton, 1905
	I	1		3			2		Hartley, 1940
....	II	2	3			4	1		Hertling, 1928
	I	3	1			2	4		Jones, 1952
	I	1	3				2		Kühl, 1963
	I	1	3		2		4		Nikolaev, 1955
	I	1	2						Steven, 1930
....	II	2					1		Gilis, 1966
	I	1	2						Jonsson, 1966
	II	3	2					1	Redeke, 1906
	I	1	3				2		Hatanaka, 1954
	I	1					2		Hatanaka, 1954
	I	1				4	2	5	Fulton, 1905
....	I	1	3	4			2		Rae, 1956
	I	1							Steven, 1930

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TABLE 1. OCCURRENCE OF FOOD ANIMALS IN FLAT FISH (Continued)

Scientific Name	Common Name	Area
Microstomus pacificus	dover sole	Pacific (USA)
Peltotretis flavilatus	lemon sole (N.Z.)	Pacific (N.Z.)
Platichthys stellatus	starry flounder	Pacific (USA)
Pleuronectes flesus	flounder	North Sea
		Baltic ....
		North Sea
Pleuronectes platessa	plaice	North Sea
		North Sea
		North Sea
		North Sea ....
		North Sea
		North Sea
		Baltic
		North Sea
		North Sea......................
		North Sea
		North Sea
		North Sea
		North Sea
Liopsetta putnami	smooth flounder	Atlantic (USA)................
Pleuronectes flesus	flounder	North Sea
		Baltic
Pleuronectes flesus luscus	flounder juv.	Black Sea
Pleuronectes platessa	plaice	North Sea
Pleuronichthys ritteri	spotted turbot	Atlantic (USA)................
Pseudopleuronectes americanus	winter flounder	Atlantic (USA)
Pleuronichthys cornutus	frog flounder	Pacific (Japan)
Pseudopleuronectes americanus	winter flounder	Atlantic (USA)
Rheinhardtius hippoglossoides	Greenland halibut	Davis Strait
RHOMBOSOLEIDAE		
Rhombosolea millari	yellow-belly flounder (N.Z.)	Pacific (N.Z.) ....
Rhombosolea plebeia	sand-flounder (N.Z.)	Pacific (N.Z.)
Rhombosolea retiaria	black-flounder (N.Z.)	Pacific (N.Z.)
Rhombosolea tapirina	greenback flounder	Pacific (N.Z.)
SOLEIDAE		
Buglossidium luteum	solenette	North Sea
Peltorhamphus novae-zeelandiae	common sole (N.Z.)	Pacific (N.Z.)................
Solea solea	common sole	North Sea
		Salt lake, Egypt
		North Sea
		North Sea
		North Sea ....
		North Sea
		North Sea
		North Sea
		North Sea
Solea lascaris	sand sole	North Sea ....
Solea variegata	variegated sole	North Sea
Synaptura nigra	black sole	Pacific (Australia)
CYNOGLOSSIDAE		
Cynoglossus semifasciatus	Malabar sole	Indian Ocean ....

Group	P	M	L	A	E	C	F	Reference
I	2	1			3			Hagerman, 1952
II	1	2				3	4	Graham, 1956
II	3	2				1		Orcutt, 1950
II	2					1	3	Hartley, 1940
I	3	1				2		Hertling, 1920
I	1	2				3		Stadel, 1936
I	2	1				3		Blegvad, 1916
I	1	2				3		Blegvad, 1930
I	2	1			3			Cunningham, 1897
I	2	1			3			Franz, 1910
I	1							de Groot, 1964
I	1	3						Hartley, 1940
I	2	1						Hertling, 1928
I	3	1			2	4		Jones, 1952
I	1							Kühl, 1963
I	1		1					Leeuwenhoek, 168
I	1	2				3		Redeke, 1909
I	2	1				3		Todd, 1915
I	3	2			1			Steven, 1930
II	2					1		Bigelow, 1953
II	4	2				1	3	Redeke, 1905
II	3	2				1	4	Mulicki, 1947
I	1					2	3	Kaneva, 1960
I	1	2			4	3	1	Redeke, 1906
III						2	1	Bigelow, 1953
II	3	4		2		1		Bigelow, 1953
I	1					2		Hatanaka, 1954
I	1					2		Pearcy, 1962
III						2	1	Jensen, 1935
I	1	2				3		Graham, 1956
II						1	2	Graham, 1956
I					2			Graham, 1956
II		1				2	3	Graham, 1956
I		2				1		Steven, 1930
I	1	2				3	4	Graham, 1956
I	1	4			2	3		Cunningham, 1890
I		1				2		El-Zarka, 1963
I	1					2		Hartley, 1940
II	3	2			4	1	5	Mohr, 1918
I	1	3			5	2	4	Redeke, 1911
I	1	2			4	3	5	Tesch, 1913
I	1	2			5	4	3	Todd, 1907
I	1	2						Steven, 1930
I	1	2				3	4	Redeke, 1906
II	2					1		Hartley, 1940
		3	2			1		Steven, 1930
I	1	2				3		Roughley, 1951
I	1	3				2		Seshappa, 1953

TABLE II

METHODS OF STUDYING DIURNAL ACTIVITY OF FISH

R - round fish F - flatfish C - crustacean

METHODS	PRINCIPLE	REFERENCE
CHEMICAL:	Analysis of differences in the consumption of oxygen during 24 hours (R,F).	Clausen (1936) Gompel (1937) Hempel (1964) Shlaifer (1939)
PHYSICAL: Acoustic	Whenever a fish moves in a beam of ultrasonic sound from or towards the transmitter, the reflected sound shows a Doppler shift in frequency.	Cummings (1963) Muir c.s. (1965)
	The electrical resistance between a pair of electrodes changes when a fish passes (freshwater, R).	Moore (1961) Swift (1960,1962 and 1964)
	The discharge rate of some species of electrical fish may be used for activity recording (R).	Lissmann c.s. (1965)
Electrical (Inductive)	Uses the induction voltage which is generated in a fixed coil when flatfish with permanent magnet crosses the coil (F).	de Groot c.s. (1967)
Mechanical	Fish is connected to recorder by a wire (F).	Spencer (1939)
	Displacement of unstable constructions (wire, pendulum, or frame) as a result of swimming cause the closing of electrical contacts (R,F).	Davis (1964) Fontaine (1956) de Groot (1964) Jones (1955) Kruuk (1963) Spoor (1941) Wikgren (1955)
	Disturbance of the equilibrium of a balance carrying a false bottom is caused whenever a flatfish rises (F).	Harder c.s. (1954) Hempel c.s. (1956)
Optical	Fish interrupts an infrared light beam.	Thinès c.s. (1965)
Thermoconductive	Swimming motions disturb the convection pattern around an N.T.C. resistance (thermistor) and cause resistance variation owing to the changed cooling (C).	Heusner c.s. (1966)

TABLE III SUMMARY OF PUBLISHED DATA ON DIURNAL VARIATIONS IN TRAWL CATCHES

Scientific Name	Common Name	Area	Time of Year	Greater catch		Catch Differential	Author
				Day	Night		
BOTHIDAE							
Arnoglossus laterna	Scald-fish	North Sea	May-Aug.(RV)	+		about 1.5 times	de Veen (pers.comm.)
Scopthalmus rhombus	Turbot	North Sea	-	+		-	Rae (1957)
PLEURONECTIDAE							
Glyptocephalus cynoglossus	Witch	Atlantic (UK)	Apr.-Oct.	+		3 times	Bagenal (1958)
Hippoglossoides platessoides	Long rough dab	Atlantic (UK)	Apr.-Oct.	+		2.5 times	Bagenal (1958)
Limanda limanda	Dab	North Sea	throughout (RV)		+	4 times	Parrish c.s. (1964)
		North Sea	May-Aug.(RV)		+	2 times	de Veen (pers.comm.)
Microstomus kitt	Lemon sole	North Sea	throughout (RV)		+	3 times	Parrish c.s. (1964)
		North Sea	throughout		+	-	Rae (1947)
		North Sea	-		+	-	Jones (1956)
		North Sea	-		+	2 times	Bregnballe (1961)
Pleuronectes platessa	Plaice	North Sea	Jan.-Feb.		+	about 2.5 times	de Groot (1964)
		North Sea	Mar.-Dec.	+		about 1.3 times	de Groot (1964)
		North Sea	Mar.-Dec.	+		2 times	Hempel (1964)
		North Sea	throughout (RV)		+	2 times	Parrish
		North Sea	May-Aug.(RV)		+	about 1.2 times	de Veen (pers.comm.)
		North Sea	throughout	+		about 1.5 times	Woodhead (1964)
SOLEIDAE							
Buglossidium luteum	Solenette	North Sea	May-Aug.(RV)		+	3 times	de Veen (pers.comm.)
Solea solea	Common sole	North Sea	-		+	-	Cunningham (1890)
		North Sea	Jan.-Jul.		+	about 3.2 times	Boerema c.s. (1952)
		North Sea	throughout		+	about 2.3 times	de Groot(unpublished)
		North Sea	-		+	about 2 times	Redeke (1905)
		North Sea	May-Aug.(RV)		+	2.5 times	de Veen (pers.comm.)
		North Sea	Mar.-Sept.		+	1.4 - 1.7 times	de Veen (pers.comm.)
		North Sea	throughout		+	2.5 times	Woodhead (1964)

R/7

They divide the fish into the following groups: (a) Fish-feeders (larger mouth sizes; heavily toothed gill raker; simple intestinal loop): (b) Crustacea-feeders (mouth size decreasing compared with the former group; "teeth on the gill rakers and more complicated intestinal loop): (c) Polychaeta-feeders (small mouth; no or few "teeth" on the gill raker and more complicated intestinal loop compared with the two former groups).

2.3 Feeding behaviour

Which prey a fish can capture depends to a large degree on its feeding habits or foraging methods. Therefore a summary of direct observations on feeding habits of several flatfishes is given. This subject is treated separately from locomotion and diurnal activity, although there is a close interrelation with these factors.

2.3.1 Post-larval stage Research on the food and post-larval fish was done by: Arndt (1964), Lebour (1919) and subsequent years, Shelbourne (1953). According to Lebour (1919) sole larvae (*Solea solea*) only feed during the night although they are active during the day. Plaice larvae only feed during the day time (Shelbourne 1953). Johansen (1925) also observes differences in the food uptake during day and night, although the number of observations from which he draws his conclusions are few. The observation of Lebour (1919) of the night feeding of sole larvae is not in accordance with the findings of Flüchter (1965 and 1966) and Rosenthal (1966). They observed via cine films that sole larvae fed during the daytime. They describe the foraging extensively. After absorption of the yolk-sac, the sole larvae stay near or on the bottom for short periods. The larvae are still quite symmentrical and they lie for some time on their side. During feeding they swim with their back upwards. They catch their food almost exclusively near the bottom. It was interesting to note that sole larvae seemed to have more difficulty in catching their prey than other fish larvae.

2.3.2 Juveniles Creutzberg (1946) describes the feeding behaviour of plaice, flounder and dab (*Limanda limanda*). The plaice is the most pronounced mollusca feeder and hence unsuited to shrimp-hunting, it lacks the stimulus for pursuing a prey. Much better shrimp feeders are flounder and dab. Creutzberg observed in the flounder a shrimp-hunting behaviour. Instead of raising his head a little from the bottom, as plaice and dab do when observing a shrimp, he squeezes his head on the bottom. He moves carefully forward on his fin-rays. Its upper pectoral fin does not move in this case.

2.3.3 Adults Observations on the feeding behaviour were made by De Groot (1966), Scheuring (1921), Steven (1930) and Weber (1965). Steven describes in detail the behaviour of the lemon sole. It feeds on polychaeta. The fish is constantly on the move, swimming for short distances and halting for short periods. When it stops, the head is raised well off the bottom as it scans its environment. Should it discover a worm, it pounces upon it with a forward leap and brings his mouth down almost vertically upon its victim. Rae (1965) concludes from the small size of the stomach and the presence of food in it at all times that feeding goes on both day and night, and that meals are small but frequent. Certain anatomical characteristics support his view. Steven further describes the feeding habits of the common sole in foraging for prey. This species is, under normal conditions, almost entirely dependent on its tactile sense. This is true for the whole group of Soleidae. Tirelli (1938) observes that taste-buds on the underside of the head are only found in this group of flatfishes. The sole creeps slowly over the bottom using its fin-rays more for walking than for swimming. The sole does not perceive a prey before it is above it. Then it stops abruptly and starts biting the prey. Stevens also describes the feeding behaviour of plaice and dab. Both are visual feeders. The dab reveals habits similar to those in the lemon sole, but does not bring his mouth down vertically on his prey. The head is not raised as far from the bottom as the lemon sole. The hunting posture of the plaice is nearer to the horizontal. De Groot has investigated several species of flatfish under experimental conditions and was able to divide the different species according to their physiological capacities into non-visual and visual feeders. The former are night feeders, the latter day-feeders. The first group almost exclusively makes use of chemoperception in localising their food, but also possess well developed vision.

To this group belongs the sole (Soleidae) which feed mainly on invertebrates which move slowly or not at all and live in or on the bottom. The second group can again be subdivided into (a) visual feeders which possess the possibility of using chemoperception in their search for food (plaice, flounder and dab); and (b) a group which find their prey exclusively visually and includes turbot (Scophthalmus rhombus) and brill (Scophthalmus maximus). If we consider the visual faculty of the different species of flatfish, we get good support for the above mentioned division (Scheuring 1921). Weber (1965) made underwater observations in the Mediterranean on two small flatfishes belonging to the Bothidae: the wide-eyed flounder (Rhomboidichthys podas) and Grohmann's scald-fish (Arnoglossus grohmanni). Both species make use of the feeding habits of asteroids. The asteroids stir up the substrate in their search for food. The mud cloud attracts both species of flatfish and they accompany the asteroids in order to seek food.

3 DIURNAL ACTIVITY

3.1 Field observations

3.1.1 Plaice Bateson (1890) and Steven (1930) observed that plaice is a visual feeder and therefore a day-feeder. This is supported by observations on stomach contents (Blegvad 1916; De Groot 1964; Jones 1952; and Petersen 1911). Franz (1910) comes to the conclusion that plaice is a day-feeder notwithstanding the fact that it sometimes feeds in the night on luminous ophiuroids (Amphiura filiformis). Hertling (1928), however, states that the plaice is a night feeder because it feeds on sand-eel (Ammodytes marinus). We may conclude that plaice is predominantly a day feeder. Tank observations seems to contradict this point of view. They always show a higher activity in the night than during the day. (Blegvad 1916; Boulenger 1929; Harder and Hempel 1954). This is due, however, to a different phase of activity, as was shown in the experiments on post larval and juveniles (Bregnballe 1961; Shelbourne 1953; Wimpenny 1960) and on adults (De Groot 1964; Hempel 1964a and Verheijen and De Groot 1967).

3.1.2 Flounder The observations on this species are nearly the same as those on plaice. Both species are closely related, as is clearly demonstrated by the occurrence of bastards (Kändler 1935). Tank observations were made by Boulenger (1929); Bregnballe (1961); Harder and Hempel (1954); and Verheijen and De Groot (1967). Observations on diurnal fluctuations in feeding have been made by Arndt and Nehls (1964). Field observations were made by Bregnballe (1961) and Hartley (1940).

3.1.3 Sole Cunningham (1890) advanced a hypothesis, based on both tank observations and the catch of common soles, that the sole feeds at night during spells of greater activity. By means of this he was able to explain the catch difference during the 24 h fishing period. The tank observations were confirmed by Bateson (1890); Boulenger (1929); Steven (1930); and Kruuk (1963). Kruuk showed experimentally that Cunningham's hypothesis was correct. During the day it was very difficult, if not impossible, to chase the sole out of the sand.

3.1.4 Other species Boulenger (1929) also observed a greater activity of dab and turbot kept in captivity during the night. Graham (1956) found the same for the New Zealand common sole (Peltorhamphus novae-zeelandiae). Mast (1914) observed the same for the ocellated flounder (Ancylopsetta quadrocellata) and the gulf flounder (Paralichthys albigutta). Starck and Davis (1966) observed that the eyed flounder (Bothus ocellatus) which occurs in the sandy areas of reefzones, were resting, uncovered, on the sand during the night. They supposed that they were feeding.

3.2 Experimental work

To study diurnal activity of fishes several methods have been used. These methods and their principles are shown in Table II. The methods applicable to research on flatfishes are discussed below.

A method based on the analysis of differences in oxygen consumption in the course of the 24 h day was used by Gompel (1937) and Hempel (1964a) for plaice. Gompel observed differences of the rate of oxygen consumption between day and night - night consumption was about 1.2 times greater. He also observed differences due to high and low water. Hempel found the same value of about 1.2 times greater oxygen consumption during the night hours. These methods show however a difference in activity in a given period, but do not describe the type of activity such as locomotion, feeding or swimming. The same objection can be raised against the balance method of Harder and Hempel (1954) and Hempel and Lillelund (1956). The methods used by Kruuk (1963) and De Groot (1964) have this disadvantage to a lesser degree. Their method is based on the displacement of a vertically suspended thread as a result of swimming, which causes the closing of an electric circuit. This signal can be used for recording. However, the height at which the fish swims is not recorded. One can use threads of different lengths. But still the method has the disadvantage of the threads getting entangled and of the fish biting off the leaden balls which keep the threads straight. This did occur in tests with turbot.

The inductive method used by De Groot and Schuyf (1967) is more advantageous. This method uses the induction voltage, which is generated in a fixed coil, lying on the bottom or hanging just above the surface of the water. When a flatfish provided with a permanent magnet crosses the coil this is registered according to the height at which it passes, i.e. just above the bottom, mid-water or near the surface. It is thus possible to differentiate between feeding and swimming activity.

Verheijen and De Groot (1967) distinguish five types of activity for sole and plaice which can be grouped into two behaviour phases - active and inactive. The five types of activity are:

(1) When the intensity of illumination decreases the inactive phase changes to active with the fish coming out of the sand in the afternoon or evening.

(2) Foraging over the bottom.

(3) At lower levels of illumination the fish leave the bottom and swim for prolonged periods some distance off the bottom.

(4) With increasing illumination in the morning the fish begin to burrow into the bottom.

(5) A period of inactivity under the sand.

3.3 Diurnal variation in the catch

Heape (1887) describes the diurnal variation in the catch of soles and other flatfishes. "Again, fishermen say that at night more soles are caught than during the daytime, while round fish rise from the bottom at night, and therefore more are caught during the daytime than at night. During the day soles and flatfishes are believed to "sand" themselves, i.e. to cover themselves over with sand". The origin of this phenomenon may be that the changes in the diurnal activity pattern of fishes reduce the numbers caught by the gear. The catching efficiency of the gear will therefore be different during day and night. During the night the avoidance of the trawl will be reduced. This is also the case for the herding effects of the bridles and trawl doors (Blaxter and Parrish 1966). It is also possible that during the night the fish will leave the bottom for prolonged periods. These theories or a combination of them may explain the catch variations shown in Table III.

The higher catch of sole could be explained by the fact that this species is a night feeder (Kruuk 1963). De Veen (1963, 1964, 1967) describes the phenomenon of soles swimming near the surface of the sea. During the nights that swimming soles are observed the trawl catches drop considerably. The soles are now in a higher phase of activity and are leaving the bottom for prolonged periods in the same manner as the other flatfishes.

However, for plaice the picture is far from clear. De Groot (1964), Hempel (1964a) and Woodhead (1964c) all give data showing higher catches during the day in the southern North Sea. There is an exception during spawning time (Jan-Feb) when the night catches exceed the day catches (De Groot 1964). Atkinson (in Hefford 1909) also found that there was a clear difference between the day and the night catches during spawning; the day catch was 33 males and 10 females per h, and at night 51 males and 7 females per h. Parrish, Blaxter and Hall (1964) show that in the northern part of the North Sea the catches are higher during the night hours. There is also the possibility that the higher catches at sunrise may be due to the cirumstance that most fishes are at that time in a hungry state and that feeding activities have just started (Bregnballe 1961 and Woodhead 1964). Day and night otter trawl fishing near Newfoundland and the Grand Bank area revealed strong evidence that the Long rough dab make vertical movements (Pitt 1966). During daylight hours they were generally on the bottom.

4 MOVEMENTS

4.1 Description Locomotion

A review of locomotion in relation to feeding has been given under "feeding behaviour, adults", (2.3.3). In connection herewith we now give a short review of the observations on New Zealand sand flounder (Graham 1956), common sole (Kruuk 1963) and starry flounder (Orcutt 1950).

4.1.1 New Zealand sand flounder, (Rhombosolea plebeia) "The long fins which fringe the edges of the body are made to undulate, that is to move up and down from head to tail in a waving manner, and this gives them their progression through the water. They are able to move with great rapidity on the floor of the sea and the zigzagging speed with which they shoot away is remarkable".

4.1.2 Common Sole At the end of the day the common sole sometimes becomes rather suddenly active. It throws the same off its back with a rather typical movement, the "Omega-jump" and then the fish begins to shamble over the bottom. The locomotion is performed through an undulating movement of the finrays of the dorsal and anal fins over the surface of the bottom. Kruuk also observed in tank experiments that there was a kind of homing, in that the fish returned toward the same depression in the sand in the morning, which it had left the evening before.

4.1.3 Starry flounder When the fish is normally in resting position the dorsal and anal fins are held at an angle toward the blind side, "... and (the fish) is therefore not resting on the bottom, there is a kind of water cushion between. This allows for escape of water from the opercular opening on the blindside". In this connection it is interesting to note the observations which Yazdani and Alexander (1967) made on the respiratory currents of flatfish. They state that normally the respiratory current is solely expelled through the upper opercular opening. Orcutt further states that the fish moves in a shambling way along the bottom "rowing" on his finrays. He also observed a backward locomotion which the fish uses when it encounters obstacles. The pectoral fins are not used in normal slow progression, but when the fish are feeding or get frightened they are expanded like open fans and used as paddles. This movement can be well observed when the fish leaves the bottom for short swimming periods.

4.2 Swimming speed

The swimming speed of fishes and its maintenance is of very great importance in avoidance of towed nets. Observations on swimming speed of several flatfishes are given by Beamish (1966), Blaxter and Dickson (1959) and Bregnballe (1961).

The influence of towing speed on flatfish catches was discussed by Boerema (1957) and experimental work with models reported by Sundnes (1963). Rosenthal (1966) made observations on the swimming speed of sole larvae and states that their swimming speed is about

300 m/h. To compare the swimming speed in fish of different sizes, the swimming speeds were calculated by Beamish (1966) as body lengths per second (BL/sec) as was suggested by Bainbridge (1958). Beamish gives for the winter flounder (Pseudopleuronectes americanus) a swimming speed of 4 to 6 BL/sec (10 to 17 min). Blaxter and Dickson (1959) give maximum swimming speeds of 4 to 5.2 BL/sec for plaice; 4 BL/sec for flounder; 1.3 BL/sec for dab and 2 BL/sec for lemon sole. Bregnballe (1961) gives a swimming speed for flounder of 1 BL/sec. The latter two references do not give data on the maintenance time of these speeds, as was provided by Beamish. Sundnes (1963) gives a theoretical swimming speed and distance based on hydrodynamic resistance and energy metabolism in the plaice. He found a speed of 4.4 BL/sec in just over 1 min. Boerema (1957) found that an increase in towing speed from 2.8 to 3.0 mph, resulted in a 20 percent decrease in catches of plaice. This is most likely due to the fact that with increasing speed the trawl tends to be lifted from the bottom.

4.3 Vertical migration

One of the main factors determining the diurnal variations in the catches may be the diurnal change in vertical distribution of flatfishes. There are many documented observations on flatfishes taken in pelagic trawl and driftnets in darkness: Graham (1956); Hartley (1940); Jones (1956); Lavenberg and Fitch (1966); Parrish and Blaxter (1964b); Woodhead (1966). Interesting observations of the common sole are described by De Veen, (1963, 1964 and 1967). Based on verbal inquiries among Dutch fishermen in the spring of 1963, 1964 and 1965, he described the phenomenon of soles swimming at the surface in the North Sea. The investigation revealed surface swimming at night which resulted in a rapid migration to the spawning grounds near the coasts of Holland, Germany and Denmark. Soles only migrated during the night and only when the tidal currents were flowing to the NE, ESE or S guaranteeing transport in the direction of the spawning grounds. They were nearly immobile, and maintained a NE and E, heading when the current was in other directions. This suggests that two types of orientation are used; selection of the appropriate tidal current, and after having reached the surface an orientation of the body independent of the tidal currents. De Veen discusses a number of possible orientation mechanisms of which the compass orientation seems to be most appropriate. It is interesting to note that already Van den Ende (1849) described the phenomenon of plaice swimming near the surface, during July near the Dutch coast but during the day. The same observation was made by Graham (1956) on the New Zealand turbot (Colistium undipinnis). He saw the turbot (not feeding) simply swimming near the surface in full sunlight.

The most pelagic of all flatfishes are the halibut, (Hippoglossus hippoglossus) and the Greenland halibut (Rheinhardtius hippoglossoides). Both species leave the bottom in pursuit of their prey. This was also been observed in the Japanese halibut (Hippoglossoides elassodon) (Suyehiro 1934). Shuntov (1966) made observations in the northern Pacific Ocean on the black halibut (Reinhardtius hippoglossoides matsuurae), which is a subspecies of the Greenland halibut (Hubbs and Wilimovsky 1964). In Icelandic waters the halibut feeds mainly on ocean perch (Sebastes marinus), and the Greenland halibut in Western Greenland waters feeds mainly on capelin (Mallotus villosus) (Jensen 1925 and 1935; McIntyre 1952). In Faroe waters the halibut feeds mainly on sand-eel (Ammodytes marinus) (Joensen 1954). Ocean perch and capelin are both pelagic species and consequently bottom feeding is insignificant. Also, both species are caught in seine nets fishing either pelagic or semi-pelagic (Boldovski 1944; Jensen 1925 and 1935; Olsen 1966). It seems probable therefore that both species of halibut are more pelagic in their habits than is usually thought. Another confirmation of this point of view is the following observation of Hansen mentioned in Jensen (1935). After tagging, the released Greenland halibut swims away with the dorsal edge (fin) upward.

Another confirmation can be found in Jensen's description of the smaller degree of assymetry, position of the one eye on the dorsal surface of the head, the color of the blind side and the developed musculature on that side. Jensen supposes that the arrest of the left eye at an early stage, when it has reached the top of the head, is a secondary adaptation to the divergent mode of life in the adult Greenland halibut, while later, the free swimming in mid-water results in color changes on the right side and for the same reason its musculature is developed. Russell (1928, 1930) made observations on the pelagic young of some flatfishes. He found that during the day most post-larvae live below 15 m, and at night they tend to move about at all depths from about 10 m downwards, but only few reach the surface. In the daytime he found for the following species, a slight preference of depth, becoming successively deeper: Turbot and brill; Norway topknot; flounder; common sole; dab; variegated sole; lemon sole and common topknot.

Barham (1966) observed in the Pacific from a diving saucer, a pelagic flatfish probably of the genus Cyclopsetta (Bothidae) at a depth of 120 m in 1300 m water.

Perhaps we can say, with Pavlov, that all animals in the course of their lives are capable of working out adaptations to their environment.

5 SPAWNING BEHAVIOUR

5.1 Description

There are few observations on the spawning behaviour of flatfishes. It is known of only two species, the plaice (Forster 1953, Riley - in Beverton 1964) and the common sole (Butler 1895, Flüchter 1965 and 1966). From their observations it seems that the actual spawning usually takes place at night. The various observations are contradictory due to the difficulty of observing spawning behaviour.

5.1.1 Plaice Forster observed the spawning of plaice one evening in the month of February. He states: "The two plaice were swimming in midwater, about 2½ ft from the bottom, the female lying slightly diagonally across the back of the male their vents being close together. The female, considerably larger than the male, was quivering violently and emitting a rapid stream of eggs. After about 20 sec the fish separated and settled on the bottom. Fertilized eggs from subsequent spawnings by other plaice were taken in the tank for the next 3 days, between 6 and 9 p.m." Riley noticed that shortly before actual spawning begins both sexes are unusually active and spend much of their time swimming above the bottom of the tank. When the female is ready to shed her eggs her behaviour changes abruptly; she stays in close contact with the substrate and is difficult to dislodge even if prodded. The male on the other hand, continues to swim actively above or near the bottom of the tank (quoted in Beverton 1964).

5.1.2 Common sole Butler describes the sole, lying on the bottom of the tank, raising its head and bringing it down with force again. The eggs appear to be shed one at a time as the result of this movement. The movement described is different from the digging-in habit. Flüchter made the following observations. The soles were swimming close to the water surface and pressed together, but swimming normally. Sometimes a head projected out of the water. The male in the upper position. The spawning was observed during the night hours.

5.2 Effect of spawning behaviour on catches

Of two species, plaice and common sole, it is known that there is an excessive shift in the sex ratio in the catch on the spawning grounds. The catches of males exceed those of females (Beverton 1964; Christensen 1960; Hefford 1909 and 1916; Simpson 1959; Wallace 1909). As to the origin of this shift several possibilities are advanced which possibly operate in combination. It may be that different behaviour of the sexes is exhibited during spawning. In this case it could be either that the number of females taken in the trawl is lower than normal or the number of males taken is greater than normal. Also, it is possible that more males are present on the spawning grounds since the females spawn in a relatively short time and leave the grounds. Beverton (1964) supposes that, to some degree, the behaviour of the male and female plaice on the spawning ground may be responsible for the difference in availability. However, the tank observations are too contradictory and too few to support this hypothesis. But there is a different behaviour between spawning and non-spawning fishes. Todd (1915) states that the cessation of feeding is prolonged by the spawning plaice. De Groot (1964) showed that the diurnal catch pattern was reversed during January to February in the spawning area. Larger catches were made during the night. He suggests that this is related to the spawning behavior. He confirms the observation of Atkinson (in Hefford 1909) based on one journey only. Hefford (1909 and 1916) and to some degree also Simpson concluded that it was more likely that the shift in sex ratio is due to the fact that the males remain longer on the spawning grounds than females.

Simpson (1959) gives, for mature fish on the Flambourough area spawning ground for 1949, a sex ratio of 4.4:1 and for the Southern Bight spawning ground for 1950 a sex ratio of 19.6:1. One should be aware, however, that through the sex-ratio variation effect, the age composition of the population is interwoven. The sex ratio among the younger plaice is about 1:1, but there is a shift in favor of the females with increasing age. Among older fish a ratio of 1:10 was found. According to Hefford (1916), this dominance of females was the result of a higher mortality among the males. Christensen (1960) showed that the males and the females of the common sole were separated in the period just before spawning.

Jonsson (1966) states for dab on the spawning ground, that the males are more abundant, they arrive earlier and stay longer. This increases the possibilities of fertilization of the eggs. The males reach maturity earlier and the reproductive organs are active for a longer period.

6 REACTIONS TO DIFFERENT STIMULI

6.1 Chemical

The first studies in detail of the sense organs of fishes in relation to their feeding were by Bateson (1890). He divided fishes into two groups "fishes which seek their food by scent" (common sole and solenette) and "fishes which seek their food by sight" (turbot, brill, common topknot, plaice, dab and flounder). Bateson concluded, wrongly however, that the olfactory organs are of no importance at all in dab, plaice and flounder. Pipping (1927) made observations on olfaction and feeding habits in the common sole, flounder and turbot. She observed the importance of olfaction and taste in feeding of the common sole, the lack of olfaction in the turbot and a slight indication of the use of it in the flounder. De Groot (1966) carried out experiments on the role of olfactorial factors in connection with the feeding in the common sole, plaice, dab, flounder, turbot and brill. He showed that the sole, a non-visual feeder, which finds its prey almost exclusively by making use of chemoperception possessed well developed vision. The group of the visual feeders could be subdivided into a group which possess the possibility of using chemoperception in their search of food, although they are visual feeders (plaice, dab, flounder) and a group which find their prey exclusively visually (turbot, brill).

6.2 Optical

In the recent publications of Nicol (1963) and Woodhead (1966) extensive reviews of the aspects of photoreception and vision in fishes and the importance of light on the behaviour of fishes are given. Therefore I confine myself here to a very short review of these aspects, notwithstanding their importance.

Bull (1930) made a successful attempt at conditioning a plaice to a visual stimulus. Scheuring (1921) made observations on the role of the eyes in feeding and estimated the field of vision of several flatfishes including dab, plaice, lemon sole, solenette and turbot. De Groot (1966) studied the role of visual and olfactorial factors in connection with the feeding behaviour of flatfishes. Holt (1895a) described the recessus orbitalis as an accessory visual organ in pleuronectid fishes. Nicol (1961 and 1965) describes the retino motorchanges in common sole, plaice and lemon sole and confirms that the eyes of flatfishes respond to illumination in the same manner as those of other teleosts. He rejects the opinions of Bayliss, Lythgoe and Tansley (1936) and Walls (1942) that only the retinal pigment in the eye of flatfishes moves. Blaxter, Parrish and Dickson (1964) and Blaxter and Parrish (1966) give for flatfish a reaction distance to ground ropes and panels of netting of 0.3 to 0.6 m.

6.3 Hydrostatic

The bathymetric distribution plays an important role in the life of flatfishes. This may be due to a preference for a given pressure or a given light intensity or possibly a combination of these. As a general rule the younger stages live in shallow water and, with increasing age, move into deeper water. This phenomenon was first described for plaice by Redeke (1904, 1905b) and is wrongly known as Heincke's Law. Heincke (1907 and 1913) described the same phenomenon for plaice. McCracken (1958) describes it for the Atlantic halibut. It is interesting to note that Wise and Jensen (1959) state that the halibut never cross deep water (Fundian and Laurentian Channels). Rae (1957) described the migration of older turbots to deeper water. Alverson (1960) studied the annual and seasonal bathymetric distribution of several important North American flatfishes including: English sole (*Parophrys vetulus*); Petrale sole (*Eopsetta jordani*); Dover sole (*Microstomus pacificus*); Starry flounder and Rocksole (*Lepidopsetta bilineata*). Gosline (1965) described the vertical zonation in the upper water layers of Hawaiian flatfishes including: *Bothus pantherinus*, *Bothus mancus*, *Parabothus chlorospilus*, *Taeniopsetta radula*, *Engyprosopon hawaiensis*, *Engyprosopon xenandrus*, *Samariscus triocellatus*, *Samariscus corallinus*, *Poecilopsetta hawaiiensis* and *Aseraggodes kobensis*.

Rice (1964) and Qasim, Rice and Knight-Jones (1963) studied the sensitivity to pressure changes in plaice larvae. They found that at a pressure of two atmospheres the larvae swam strongly upwards and were soon found in the upper half of their experimental tank. Further they found that with increasing pressure the larvae swam towards a light source and that decreased pressure caused a movement away from the light or a decreasing swimming activity. We may conclude that flatfishes, when they grow older, move to deeper water guided by light or pressure or perhaps a combination of the two. There seems to be some experimental evidence that pressure plays an important role. The depth at which most flatfishes live varies from 0 to 200 m. Exceptions are the halibut species and the species caught on deep-sea expeditions (about 1000 m).

6.4 Sound

To study the hearing possibilities of flatfishes Maier (in Von Frisch 1936) tried to get spontaneous reactions from the common sole and turbot, but failed as did Bull (1928) with plaice and flounder. De Groot (unpublished 1962) succeeded in conditioning plaice and flounder to sound of 200 and 400 Hz. The blinded fish were rewarded with food or punished with an electric shock (0.09 V/cm in the water).

Freytag (1961) studied the spontaneous sound production in plaice, flounder and sole. These flatfishes make noises during feeding when they suck in their food and by rapid swimming. These sounds are, however, not specific at least not for the species studied. We may conclude that little has been done in this field.

6.5 Temperature

Redeke (1904) described the migration of plaice to deep cooler water when the temperature reaches 15°C. The common sole reaches the northern limit of its distribution in the southern North Sea. It has been demonstrated (Anon. 1965), that the Danish and German sub-populations of the sole move further southward and to deeper water in wintertime as compared with the Belgian sub-population living near the Channel. These migrations are based on temperature preferences. Woodhead (1964 a,b and c) studied the changes in behaviour and in catch of the common sole during cold winters and also gives observations on other species of flatfish (dab, plaice, brill, turbot and solenette). Exceptionally large catches of sole were made during very cold winters in the North Sea. Woodhead suggested that soles are very sensitive to low temperatures and that there is a direct relationship between winter catches of soles and water temperature. Large quantities of dead or moribund soles were sometimes caught in these periods. This was especially the case when the surface temperatures went down to 2°C. The explanation of this phenomenon could be that extremely low temperatures produce physiological changes which makes it impossible for them to dig in and thus escape the trawl.

Hoff and Westman (1966), made experiments on the temperature tolerance of the winter flounder. They found a cold limit between 1°C and 0°C and a maximum temperature tolerance of 28°C (during 24 h 50 percent survived. Waede (1954) made experiments on the thermo-resistance of plaice and flounder. He saw no changes in behaviour up to 25°C, but at higher temperatures the fishes became agitated, and at 31°C they died – plaice sooner than flounder.

6.6 Salinity

Most of the flatfish belonging to the Pleuronectidae reveal very well developed osmotic adaptations. They live in the sea, but also in estuaries, rivers and lakes. Examples are the arctic flounder (Liopsetta glacialis), flounder, starry flounder and New Zealand black flounder (Rhombosolea retiaria adams) (Graham 1956 and Orcutt 1950). Other species such as turbot and long rough dab (Hippoglossoides platessoides) penetrate from the open seas with lower salinities (Kändler 1944 and Segerstråle 1965).

Remarkable osmotic adaptations were shown by the common soles transplanted to a salt-lake in Egypt. They survived and this led to a self-supporting stock (El-Zarka 1963). Parry (1966) reviews in her extensive article the physiological problems of the osmotic adaptations in fishes. All fishes used in the experiments were flounder-like species. Dakin (1908) on flounder; Dekhuyzen (1905) on plaice; Henschel (1936) on plaice and flounder; Hickman (1959) on starry flounder; Holliday and Pattie Jones (1967) on larvae of plaice; Lange and Fugelli (1965) on flounder; Motais (1961 a and b) on flounder and Waede (1954) on plaice and flounder.

6.7 Hydrographical and meteorological observations

Bull (1952), Fleming and Laevastu (1956) and Tait (1952) have given detailed reviews of the knowledge of fish behaviour in relation to hydrography. They give some references on flatfishes although their work is of a more general character.

There are some observations of catch differences during ebb and flood tides. Variations due to tidal effects are difficult to observe because other factors often mask this effect. Johnstone (1903) observed differences in catches of plaice due to the state of tide. He noted higher catches on spring tides than on neap tides. Wimpenny (1960) studied the differences in hauls of young plaice and dabs off the English East coast. When he compared hauls taken around high water with hauls taken around low water, the former contained more plaice, though of smaller size, but fewer dabs.

Hempel (1964b) made some observations on tidal effects in catches of plaice and dab in the German Bight, but did not succeed in demonstrating a clean-cut effect of tides on the catch, not even in coastal waters. Johansen (1907) gives an explanation for the differences between plaice catches in Taunis Bay and on the Northern side of Skagen (Denmark) after heavy SW, W or NW gales. The plaice are driven out of the shallow water of Taunis Bay or squeeze themselves to the bottom. This might be the explanation, but work done on herring by Walden and Schubert (1965), demonstrates how careful we must be.

Some commercial herring fishermen believe that speed and direction of the wind influence the catch. After the examination of a huge quantity of observations, it was found that only in a few cases was direction and velocity of the wind a significant factor.

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APPLICATION OF OBSERVATIONS ON FISH BEHAVIOUR FOR FISHING METHODS AND GEAR CONSTRUCTION

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Abstract

The knowledge of fish behaviour by practical observation and experience often results in the development of very specific fishing methods and influences the design of fishing gear. Examples given here show how the habitat and behaviour of fish can influence fishing operations such as attracting, frightening etc. Also some examples show how far fish behaviour can influence the selection of material and netting, as well as the construction of guiding implements and non-return devices. Synthetic fibres for fishing gear made the consideration of fish behaviour much more important than it was in the days of natural fibres.

R/8

APPLICATION D'OBSERVATIONS SUR LE COMPORTEMENT DU POISSON AUX METHODES DE PECHE ET A LA CONSTRUCTION DES ENGINS

Résumé

La connaissance du comportement du poisson acquise par l'observation pratique et l'expérimentation permet fréquemment la mise au point de méthodes de pêche bien détérminees et influe sur le dessin des engins de pêche. Les exemples fournis montrent comment l'habitat et le comportment du poisson peuvent jouer un rôle dans les opérations de pêche, par exemple sous l'angle des réactions d'attraction, d'effroi, etc. En outre, certains exemples indiquent à quel point le comportement du poisson peut influer sur le choix des matériaux et des nappes de filets, ainsi que sur la construction des dispositifs destinés à guider le poisson ou à l'empêcher de rebrousser chemin. Depuis que l'on fabrique des engins de pêche en fibres synthétiques, il convient d'attacher beaucoup plus d'importance au comportment du poisson qu'à l'époque des fibres naturelles.

APLICACION DE LAS OBSERVACIONES SOBRE EL COMPORTAMIENTO DE LOS PECES A LOS METODOS DE PESCA Y CONSTRUCCION DE LOS ARTES

Extracto

La adquisición de conocimiento del comportamiento de los peces mediante la observación práctica y la experiencia, da por resultado el empleo de métodos de pesca muy especificos e influye en las formas del equipo de pesca. Los ejemplos que da el autor demuestran cómo el habitat y el comportamiento de los peces pueden influir en actividades pesqueras como atraer, ahuyentar, etc. Otros ejemplos demuestran hasta que punto el comportamiento de los peces puede influir en la selección de materiales y paños para redes, así como en la construcción de dispositivos de guía y de los que no pueden escapar los peces. El empleo de fibras sintéticas en los artes de pesca da much más importancia al examen del comportamiento de los peces que la tenía en los días de las fibras naturales.

1 INTRODUCTION

The catch in fishing depends, as in hunting, on sufficient knowledge of the behaviour of the quarry. Only fishes are referred to here, although other animals and aquatic plants form the basis of some fishing industries, and legislative bodies often use the term "fish" for all of these.

Knowledge of the natural behaviour of fishes and of the possibilities to cause, by artificial stimulation, a certain favourable behaviour of the fishes to be caught, is so important that fishing can be considered a kind of applied behaviour research. Our present knowledge of this subject has been gained chiefly by observation of the typical behaviour of fish in their natural surroundings since before recorded history. Long before the term "behaviour research" was invented fish behaviour was observed and utilized to advantage (Mohr 1964 b). But a more detailed knowledge of the stimuli which affect fish might be helpful in designing more effective gear and methods (Westenberg 1953). This paper summarises some items of knowledge of fish behaviour which are well known to commercial fishermen in different parts of the world.

2 FISH BEHAVIOUR AND CLASSIFICATION OF FISHING GEAR

In considering the importance of fish behaviour in relation to fishing gear and methods I have found it helpful to use a classification based on types of gear rather than methods. Umali (1950); Burdon (1951); v. Brandt (1952, 1953, 1957, 1959 and 1964) are a few authors who have dealt with the problems in the classification of fishing gear. The following terms (v. Brandt1964 a) will be used in this paper and reflect the behaviour of the fishes involved:

1. Fishing without gear - Littoral fish can be taken by hand when such fish live in burrows, during droughts, are stranded ashore or in pools; and in rare instances fish in water can be grasped by divers or trained animals.

2. Wounding gear - various types of spears, harpoons and other thrown or cast implements.

3. Stupefying methods - Mechanically, chemically (fish poisoning) or electrically (electrical fishing).

4. Fishing with lines - Lines without or with hooks, baited or unbaited are used in handlining, setting, trolling and driftlining.

5. Traps - Knowledge of fish migrations, habits of seeking cover, escape reactions and their food, influence the design of small traps, large weirs and pound nets and mechanical traps.

6. Aerial traps - Gear are used to stimulate and catch fish with jumping and "flying" (gliding) habits.

7. Bag nets with fixed mouth - Scoop nets and stownets, pushed through water or set to take advantage of currents and fish migrations, are often designed with some non-return device.

8. Dragging gear - Fish that aggregate or school can be caught with dredges or various bottom, midwater and surface trawls, using a knowledge of the vertical migrations and other habits of fish.

9. Seine nets - From shore and sometimes with boats, fish on a place limited by the size of the gear can be herded into a net.

10. Surrounding nets - These, especially the purse seine and its closing gear surrounding the schools of the fish also from below, can be used over great depth.

11. Drive-in nets - Fish can be chased or guided (by lights) into shovel shaped nets which then close.

12. Lift nets - After fish swim or are attracted into position over the net, it is lifted vertically, fish wheels, used in salmon fisheries are included here.

13. Falling nets - Cover pots and cast nets are thrown over the fish from above.

14. Gill nets - Some fish seeking food or migrating are meshed when penetrating an inconspicuous net of appropriate mesh size, which may be set on the bottom, suspended at a chosen depth, or be allowed to drift and "filter" fish from a large mass of water.

15. Tangle-nets - Fish become entangled in light and loose netting because of their violet swimming reaction when touched by the net. Such nets may be single or three-walled trammel nets.

3 EXAMPLES OF INFLUENCE OF ENVIRONMENT ON FISHING GEAR AND METHODS

Successful fishing depends largely on a comprehensive knowledge of fish behaviour in order to find the fish, employ the appropriate fishing tactics and correctly design the necessary gear. The horizontal and vertical distribution of fishes has a prime influence on the fishing methods and design of the gear. Knowledge of the regular daily or seasonal migrations, temporary or usual formation of schools and the influence of environmental conditions (temperature, oxygen, salinity, light etc.) on the abundance of fish, is often a prerequisite for operating a fishery. The influence of the habitat of fish on fishing techniques may be explained by examining two of the most important factors; the depth of water and the current.

3.1 Influence of depth

The most primitive type of fishery, that of simply gathering fish by hand, depends upon a knowledge that fluctuating water levels, both in the sea and inland fishing areas, result in fish becoming stranded on dry land. Some species, such as lungfish, actually bury themselves in the mud where they can survive long periods of drought and are dug out by experienced fishermen.

Capturing fish by stupefying such as eel pouts by striking the surface of ice with a hammer, depends upon an understanding of the behaviour pattern of these fish, i.e., that they move into shallow water to spawn under the ice before it melts. In such a place they are easy to locate and are within the concussion range of hammer blows (v. Brandt, 1964 b, p.19).

Deep water, or places where the current is strong, are unsuitable for the use of poisons which stupefy fish. A special way of fish poisoning also in deeper water is to fill bait fishes with poison and place them in deeper water where larger fish will prey upon them (Weule, 1922).

In line fishing operations, a knowledge of the depth at which fishes occur influences the length of line and the amount of weight to be used. It remains a puzzle how primitive handline fishermen, without the aid of fish-detecting devices, managed to locate fishing grounds in more than 100 metres depth in places far from the coast (Millot, 1954; Treide, 1965): the gradual pursuit of fish from shallow water into such places is not possible in many cases and can give no explanation.

Fishing with mechanical and non-mechanical traps, like pots and pound nets fixed by poles is usually limited to shallow water, but sometimes large weirs and pound nets are used in deeper water with floats and anchors instead of poles. Such floating traps are employed to catch salmon, tuna and eels. Smaller traps, such as the special types of baskets used in the Mediterranean, can also be set in very deep water by anchoring them to vertical ropes.

The efficiency of most types of bag nets with fixed mouth is reduced in greater depths, but large stownets, normally attached to stakes, have been modified for use as swing nets from anchors or boats. In this way Koreans operate stownets (ankang-mang) with specialized vessels even far out to sea(Park, 1963).

The design of gear in drag-net and seine net fisheries is greatly influenced by the depths inhabited by fish schools. The height of a net and width of its mouth depends upon whether demersal or pelagic fish are sought. Pelagic trawls have been developed which can pursue fish in any depth of water (Schärfe, 1960, 1964). Efforts to create a drag-net fishery beyond depths of 1,000 metres have been described by von Seydlitz (1966). Besides influencing net design deep water fishery makes special demands on deck equipment (winches) and the towing power of a fishing vessel.

Surrounding nets such as purse seines are especially shaped to suit the depth in which fish schools occur. When using surrounding nets the fishes' behaviour can be influenced by using lights to keep fishes on the spot, and using bait to attract and concentrate schools from deep water as in the French Sardine Fishery and the purse seine fishery for tuna off West Africa (Guicheney, 1964; Da Costa and Braganca, 1965).

By setting the nets in large forms on boats and adapting the shape and handling techniques, the lift net fishery has been extended from shallow water into deeper offshore areas; as in the Philippine Basnig fishery (Rasalan, 1959) and the Japanese "stick held dip net" fishery (Nomura, 1962).

Fishing with falling nets is usually employed only in shallow water but in the Turkish Black Sea cast nets are used in depths of as much as 150 metres. This owes its success, however, to special handling rather than a change of design (v. Brandt, 1964, p.161).

The techniques of using gill nets and tangle-nets are greatly influenced by the depths inhabited by fish. In deep water such nets can be anchored on the bottom, or adjusted to hang at various levels between the bottom and the surface. In the Baltic salmon fishery when the distance between the sea's surface and the net was reduced the number of young salmon in catches increased. In Japan and in the Mediterranean Sea certain nets have a lower part of trammel net to catch large demersal fish and an upper part of small meshed gill net to take small pelagic species (compare Gouret, 1943;) Burdon, 1954; Rubio, 1955; v. Brandt, 1960, 1964 a, and 1966). This is a striking example of the influence of fish behaviour and depth on gear construction.

3.2 Influence of current

Current and the behaviour of rheophile fishes is responsible for the development of special types of fishing gear and the adjustment or adaptation of other gear to suit these conditions.

In rivers with a strong current, usual traps cannot be used but tubular traps without funnel can be used in which the fishes are pressed by the current. Also fish-barriers and fences can filter fishes moving either with or against the current. Similar equipment has been developed in Japan, California and Mexico (v. Brandt, 1964 a, p.68). Falling nets are less suited for catching rheophile fishes, but a special large cast-net has been adapted for use in some European rivers, e.g. Schleifgarne in the river Rhine.

In the bag net fishery scoop nets have been adjusted to the requirements of the salmon fishery in waterfalls of the Columbia River. Large stownets are used primarily in rivers and estuaries where there is a suitable current. Only in rare instances are bag nets operated from boats at sea (Park, 1963). A special form of lift nets, called fish wheels, have been developed to operate in a strong current to catch fish, such as salmon.

Gill nets and tangle nets can be constructed in such a way as to make them drift, attached on floats or boats when the current is not too heavy.

These examples may be sufficient to demonstrate how environmental factors can influence fishing methods and the construction of fishing gear.

4 DEVELOPMENT OF FISHING METHODS IN RELATION TO FISH BEHAVIOUR

The measures used for luring fish into a position which facilitates their capture will, in this paper, be given priority over a consideration of the handling of the fishing gear, as the former is of prime importance. The tactics to bring fish into a favourable position opposite the gear depend on the type of fish, their physiological condition, the seasons, and even the time of day. In commercial fisheries these tactics concern fish schools mostly, but sport fishermen sometimes take into consideration the behaviour of an individual fish. In the Danube River fishermen use a special type of mechanical trap to catch individual salmon (Bruschek, 1962).

The tactics used can be grouped under the following headings:

(a) attracting and concentrating fish into the range of fishing gear;

(b) frightening fish away from a position unfavourable for their capture;

(c) inducing fish to jump from the water;

(d) stupefying fish to prevent their escape.

4.1 Attracting and concentrating fish into the range of fishing gear

Bait in a broad sense, both natural and artificial, is used for attracting fish by stimulating the so-called "prey complex" (Brock, 1950). They are also attracted by sexual stimulation. Acoustic attraction can also be used beneficially. Another method is to offer hiding places to guide fishes to where they can easily be captured. Bait can stimulate various senses at the same time and can both attract and concentrate fish, particularly when intense stimulation (light and electricity) alien to fish is used. The following types of "bait" are delineated in their order of importance:

(a) chemical bait (stimulating the senses of smell and taste);

(b) optical bait (stimulating effect by movement, shape and colour);

(c) acoustical bait (stimulating effect on the acoustic nerve and tactile sense);

(d) electrical bait (stimulating effect on an ability to perceive electrical current);

(e) "bait" in the form of hiding places (stimulating effect inter alia on tactile sense).

Chemical bait - Attraction to food is probably the earliest bait used in both fishing and hunting. Before hooks and lines were known, bait was employed to attract fish (Augur, 1894). This practice is still used in Polar areas (Rasmussen, 1946). Edible bait stimulates the senses of smell and taste. Most lines, as well as some mechanical or non-mechanical traps, are baited. Occasionally, bait is also either fastened to gill nets or placed near them, to lure fish into their catching range (Hickling, 1931; Thurow; Le Gall, 1935). Besides long line fishing, and pole-and-line fishing for tuna-like species, other highly developed and modern fishing techniques, such as purse seining, are also dependent at times upon the attraction of such natural bait as live sardines (Guicheney, 1964; Da Costa, 1965). The procurement of natural bait for commercial fisheries where it is needed in large quantities is extremely difficult, and it is surprising that efforts to substitute artificial bait have hitherto failed. Odorous substances used in sport fishing have been tested in commercial fishing. Anise is sometimes used in long line fishing. Substances comprising anise, camphor, civet, musk, cinnamon and vanilla have been tested, but laboratory experiments have not yet yielded results which could be adopted in commercial fisheries (Schoeniger, 1951; Schärfe, 1954).

Chemical stimuli originate not only from the nutritional field, but are combined at times with optical or sexual stimulation. On the Upper Rhine, salmon are attracted into traps baited with live or dummy salmon of the opposite sex. In the Ayu line-fishery in Japan living fish are tied to attract fish of the same species which are then caught by the hooks. Also, in the Far East and the Mediterranean area it is known that male octopi can be attracted into small cages baited with female octopi. In the European basket fishery for eelpouts, particularly good catches are made during the time of copulation by placing a specimen in the basket (Menzenbach, 1958). It is not known whether the other fishes are attracted optically by the formation of schools or chemically by sexual substances.

Although no artificial bait is yet used to stimulate the chemical, olfactory or sexual senses of fish, recent discoveries of fish-attracting substances (Alverson and Wilimovski, 1964) and the ability of salmon to return to their home rivers chiefly by detection of minute traces of odours, are promising.

Optical bait - These attract fish either by their shape, colour and especially by their reflection of light and are used in all types of line fishery. With the trolling lines natural or artificial bait (such as fishes, insects, plugs, artificial flies) attract predators not only as a result of their appearance, but also by their movements, similar to those of exhausted prey, which stimulate the tactile senses. A blinking hook, piece of white cloth, tin-foil, a spinning or reflecting spoon, are effective artificial bait. Bait or hooks painted with fluorescent substances can attract the fish. In Vietnam phosphorescent organs of Cephalopodes are tied to the hooks to attract fish (Gruvel, 1925; Serène, 1956). Faintly luminous bait is sometimes used by sport fishermen. Experiments to achieve better catches with faintly luminous nets in the herring fishery have been unsuccessful so far.

Reflecting objects such as bits of glass or mirror have been used for a long time to catch squid and octopi (Lane 1960). The same effect can be achieved with light-coloured shells (Nishimura, 1964).

In the North Sea, mackerel fishing with gill nets decorated with tin-foil has been tested unsuccessfully. But optically baited gill nets are known in some Near East fisheries (Thurow).

The attractive effect of light is utilized on a large scale in the so-called light-fishery. There exist few fishing methods which do not use light for attracting the fish (Schärfe, 1953).

Artificial light is used for gathering fish in shallow water fisheries. Even in the Japanese fishery with cormorants, light is used at night to attract the prey. In fisheries using wounding gear - spear fishing in particular - light is used in inland waters and in the sea. Combined electric and light fishing - light to attract fish and electric current to stun them - is used by the Russians in connection with fish pumps. They have experimented with these methods in the Far East to catch saury (Nikonorov, 1964). In the Caspian Sea kilka fishery, light alone is used to attract fish to the pump head; electricity is not used to stun them (Nikonorov, 1959; v. Brandt, 1967). Besides the previously mentioned luminous bait, artificial light is also used in line fishing. Light attraction has been proposed to guide fish into traps and baskets (Sasaki, 1959). Lamp-chains as guiding fences extend the catching range of some gear. In the bag net fishery, scoop and landing nets are used for catching fishes and squids which are attracted by light. With dragged gear light is apparently impossible for attracting purposes. Artificial light has been used with seines in Yugoslavia where sardines can sometimes be concentrated by light at a distance of 0.5 to 1.0 miles offshore, and then, by means of light, be brought into shallow water where they are caught with a beach seine (v. Brandt, 1964). For the fishery at night with surrounding nets, artificial light is of decisive importance. This applies particularly to sardine and mackerel fisheries with lampara nets, purse seines, etc. Light sometimes is used in the so-called drive-in fishery to guide fish into the nets. Light is essential in dip-net fishery such as the Chinese dip-net in rivers and off beaches in South Asia, the Japanese stick-held dip-nets, and the dip-nets which catch kilka in the Caspian Sea. No examples are known of artificial light being used together with cover nets, nor with gill nets or tangle nets, but this might be done by attracting the fish after setting the nets.

Artificial light is used in the form of both surface lamps and submerged lamps, the latter type being more advantageous (Kristjonsson, 1959). Numerous investigations have been made, particularly by Japanese and U.S.S.R. scientists, dealing with the problems of the most suitable intensity and wave-length of light (Kawamoto, 1959; Inoue, 1963; Kuroki, etc., 1964). Under-water lamps of white light with an intensity of 2000 watts have been successful in catching sardines and anchovies (Kurc and Blancheteau, 1966).

The reasons why some species of fish are attracted to light have been investigated and the explanation given by Verheyen (1959) seems the most plausible: namely, that the abnormal conditions of the artificial light cause a disorientation of the fish. (A similar disorientation has been observed with birds crossing brightly illuminated towns during their nocturnal migrations). Other explanations mentioned are curiosity, positive phototaxis, seeking a preferred intensity of light and certain reflexes (Mohr, 1964 b). Investigations have also been made to determine to what extent the behaviour of fishes changes as a result of their physiological condition or of external factors (temperature, salt content, transparency of water, abundance of plankton, etc.)

The reaction of fishes to light is not constant, but it changes with the type of light and other factors (Beliaeva and Nikonorov, 1961).

Acoustic bait - Acoustic bait is seldom used, but some fishes are said to be attracted by sounds (Westenberg, 1953). There are patents on methods to attract fishes with vibrations of natural or artificial lures, e.g. Hass, 1952). Yellow-fin tuna are possibly attracted by complex sounds of low frequency (Tester, 1959). It is not yet known whether the auditory organ alone is effected or whether and to what extent the tactile sense of the lateral line is also stimulated by acoustic bait (Cushing, 1959). It is well known that some species of fish are attracted by sounds which are similar to those produced by their prey; e.g., the beating and sprinkling of water (such as in the pole and line fishery for tuna) is said to simulate the sound of jumping fishes. Shark rattles made of coconut shells used in South Asia and Oceania, are supposed to cause vibrations resembling wounded prey. From the U.S.S.R., literature has described vibration apparatus used with rods and lines by sport fishermen. These "sound baits" are sold to amateur fishermen under trade names such as "sonic fish call". (Shemanskiy, 1958, 1966; Cyprinus, 1966). Trolling lines sometimes have, in front of the hook, bait cans containing both aromatic substances and noise producing apparatus.

Successful experiments have been made to attract sharks by replaying noises made by their prey (Nelson and Gruber, 1963). Sharks can be attracted in this way from long distances, and other stimulants, olfactory and optical ones, strengthen their search for prey. Sharks are attracted by the noise of submarine explosions (Davies, 1964) and Greek fishermen exploit this habit in their shark fishery. The explanation has been given that sharks have learned to go to an area where an explosion has taken place, knowing that prey can easily be found in such places. This is a sort of self-training and it resembles the case where fishes kept in ponds are taught to react to whistle signals.

A genuine attraction of fish by the imitation of noises is said to be produced in South Europe by the "Quakholz". Similar devices are also used in the U.S.S.R. and Hungary (Wolf, 1966). They are supposed to produce the noises resembling those caused by frogs jumping into the water and are effective in attracting sheat-fishes which approach the lure and then take a hook baited with a frog (Antipa, 1916).

Electrical bait - It is not certain if electrical bait attracts fish in the same manner as acoustic bait. Shemanskiy (1966) writing about sport fishing proposes that weak electrical fields attract fishes and can even produce galvanotaxis. Spoons composed of different synthetic substances ("Electrets") or of bimetals: copper/zinc ("Electrines") are used for that purpose.

Fishes which possess powerful electric organs use electricity for detecting and catching their prey but is is doubtful that they can stimulate a positive galvanotaxis (Harder, 1965). But both in the sea and in freshwater, positive galvanotaxis is utilized in electrical fishing with direct current (Meyer-Waarden and Halsband, 1965).

Hiding places for attracting the fish - The provision of hiding places to attract fish is a widespread practice: this includes not only caves where fish can hide, but also shelters and fixed points where fish assemble.

In Madagascar, fishermen excavate artificial caves into which eels are attracted. Shelters in the form of brushwood-bundles are probably used in all continents (v. Brandt, 1964 b). Many traps and baskets work on the principle of fish entering them to take shelter and then not being able to escape.

Floating rafts such as those used in the Mediterranean (Malta and Balearic Islands), Japan and Central America, attract Dolphins (Coryphaena hippurus) in particular (Burdon, 1954, Kojima, 1956; v. Brandt, 1966 b; Hunter and Mitchell, 1966). Tuna, pilot-fish and several other species are also attracted to such shelters.

Malayan fishermen use lure-lines consisting of palm leaves attached to a rope which is stretched between an anchor and a float (Westenberg, 1953). When fish are sufficiently concentrated around these shelters, they are captured by lines or surrounding nets. But there is some doubt if fishes are attracted by the lure lines as hiding places or if other stimuli like vibrations etc. are responsible for the effect of fish concentration.

4.2 Frightening fish into the range of fishing gear

A few fishing methods operate on the principle of frightening fish either directly into the fishing gear or at least away from an area where they are difficult to catch. This can be effected by the following means, which are shown here in their order of importance:

(a) acoustic

(b) optical

(c) electrical

(d) chemical

Acoustic frightening - The practice of frightening fish by splashing water, knocking boats or calling above the surface of the water is widely spread and is used particularly in the "driving-in fishery". Noise is also used to prevent fish from evading moving fishing gear, such as surrounding nets or from escaping the gear before it is finally closed, as in the case of purse seines. Californian purse seiners have special metal plates on the ship's side and these are beaten with a hammer to keep the fishes from escaping the net (McNeely, 1961). Dynamite is also used for the same purpose in connection with purse seine nets and Philippine dip-nets (basnig). There are some patents on apparatus which frighten fish by artificial vibrations typical of predators (Früngel, 1956).

A typical fishing method exploiting the effect of noise is the "Klapper" (rattle)-fishery, formerly used only in "Kurisches Haff" (East Prussia), but which, since the last war, has spread along the western coast of the Baltic (Wolff, 1966). For this method an oak board is pushed for half or three-quarters its length into an ice-hole and by beating the upper end, fishes are driven into nearby gill nets set under the ice. Fishermen believe that fish are attracted, but as the catches in a certain place decrease after it has been fished for some time, it seems that fishes might actually be frightened away by this unusual noise. It has been suggested in the U.S.S.R. that submarine noises might cause fish to flee from higher water level down near the ground into the catching range of trawls. Echosounding observations proved that herring descend into deeper water when subjected to sudden noises or to a change of existing noises, such as those caused by motors and propellers.

Optical frightening - Optical stimuli are more important for attracting than for frightening fish, but many species are known to react with a negative phototaxis, depending upon the intensity of light and its wave length. Light-chains are used for guiding as well as for repelling fish and frightening them into non-illuminated fishing gear. This principle could be exploited to catch eels which react with negative phototaxis (Hölke, 1964). In a similar way, eels could be guided into stownets as they ascend rivers. The observations on which these ideas are based were made at the beginning of this century (compare Schärfe, 1953). A combination of light and noise has been suggested for producing a frightening effect.

In the case of drag-nets attempts have been made to increase the frightening effect of otter boards by attaching search lights to them. Attempts have also been made to use lights to drive herring from the surface into deep water. Perhaps the only case where the frightening effect of light is used in a modern fishery is found in connection with purse seines where surface and also submarine flashing lamps are used frequently to drive fishes away from the aperture of nets prior to their complete closure.

"Air bubble curtains" also fall into the category of optical frightening equipment. They have been used to drive herring schools from deeper water to fishable locations, or to drive fish from areas beyond the reach of purse seines (Smith, 1961 and 1964). Attempts have also been made to use air bubble curtains in the form of "net-less purse seines" (Smith, 1964). It was found that such air-curtain gear can be used for guiding fish, but that in a panic, the fish break through the bubble curtain (Mohr, 1960).

Electrical frightening - Electrical current in the form of electrode-chains is used to prevent the migration of fish either to or from certain areas of freshwater, as well as to keep fish from invading the entrances of turbines and pumps, and also to guide or frighten fish into fishing gear. In freshwater fisheries, so-called "cathode-nets" have been used to frighten fish from places where they cannot be caught and into baskets and nets. Such nets are made by plaiting copper wire into the lead line of an ordinary net and connecting this to the negative pole of an electric unit. A scoop net made of wire usually serves as the anode. With this type of gear, fish can be driven towards a net blocking a stretch of river and then caught from there, or the blocking net can be replaced by certain types of stownets or trap-nets which also act as a cathode (Meyer-Waarden and Halsband, 1965).

Chemical frightening - Frightening of fishes by the use of chemicals is of little importance in commercial fisheries. Chloride of lime, copper vitriol and salt are used in some countries to drive fish and squid from their hiding places (Turner and Sexsmith, 1964). Freshwater is often sufficient to scare octopi out of hiding places. Chemicals such as copper/acetate etc., have been tested inconclusively as shark repellents (Eibl-Eibesfeldt, 1959). Plant poisons and certain substances of animal origin are sometime used to frighten fish with the object of catching them. Fishes' blood and other substances secreted by their skin are supposed to frighten some fish, while attracting others, but this has not yet been used in commercial fisheries.

4.3 Inducing fish to jump

Many species of fish jump from the water to capture prey. Certain fish, as well as squid and some species of shrimp, are also able to leap over obstacles or to leave the water for short distances to escape predators. Although such habits sometimes hamper normal fishing methods, there are instances such as in mullet, salmon, and to a lesser extent in shrimp, fisheries where the jumping habit of fish has been exploited to advantage.

Artificial obstacles are sometimes placed in the water and fish are caught in mid-air as they attempt to surmount these (v. Brandt, 1964 a). Salmon are sometimes shot with a shotgun as they leap over small artificial fences. Another example is found near some waterwalls where special equipment is used to catch salmon which fail to surmount such natural obstacles (Went, 1964)

Grey mullet are caught in parts of the Mediterranean, Black and Adriatic Seas, as well as in South Asia by floating mats or so-called verandah nets. Under these vertical netting is hanging as a barrier. Mullet are caught when they leap the barrier jumping on the mat or vertically floating netting. (v. Brandt, 1960; Hickling, 1961).

In parts of South Asia and at Madagascar, mobile boats sometimes with a white reflecting underwater board attached to their sides are used to catch jumping fish. Blache et al. (1962) described a stationary canoe with matting wall from Lake Chad which works on the same principle.

Flying fish can be induced to jump at night with the aid of torches and they are caught in mid-air with scoop nets - a method which requires a knowledge of fish behaviour and skill.

4.4 Stupefying

Stupefying or narcotizing fish to prevent their escape can be carried out by the following means:

(a) mechanical

(b) chemical

(c) electrical

Mechanical narcosis - Besides the previously-mentioned methods of stupefying fish which live under ice or stones, by hammer-blows, explosives are also effective in stupefying or killing fish. The effects of these methods may, however, last for only a short time and fishermen realise that the fish must be collected before the effect of the concussion disappears. Meyer-Waarden (1966) has pointed out that such stupefied fish which regain consciousness and escape might subsequently die as a result of internal injuries.

Chemical narcosis - Chemical means are more important than mechanical ones in stupefying fish. There are many types of natural vegetable poisons, especially in the tropics, which have this effect. In dilute concentrations, such substances have a frightening effect, but in a more concentrated form they are capable of killing fish by affecting the nervous system and by destroying the protoplasm. Rotenon is one of the common plant poisons which is important in modern fish farming, where it is used to eradicate undesired species from ponds.

In comparison with vegetable fish poisons, those of animal origin are rare. Gallic acid from various animals is one example. Another is the water in which black trepang has been boiled (Nishimura, 1964).

Electrical narcosis - Electrically induced narcosis is of particular importance in freshwater fisheries. When direct current is used, fish swim towards the anode (galvanotaxis) and can then be stupefied, or even killed (Galvano-narcosis). With alternating current fish do not swim towards the anode, but they take a position vertically at right angles to the current flow (oscillotaxis) where they are stupefied (electro-narcosis). The introduction of impulse-current which has a greater physiological effect was a great advancement (Meyer-Waarden and Halsband, 1965). Electrical fishing is an indispensable method for harvesting fish in obstacle-laden rivers and freshwater lakes.

5 FISH BEHAVIOUR AND GEAR CONSTRUCTION

As one would expect, fish behaviour is generally considered when devising tactics which aim at catching particular species, but biological factors, which have hitherto often been neglected, are equally important for the designing and constructing of fishing gear, (Parrish and Blaxter, 1964). The reproach of H. Major (1947) to his sport fishing colleagues, often applies also to commercial fishermen: "Unfortunately, too many of these fishermen centred their attention on new-fangled fishing gadgets and failed to consider the why and wherefore of the daily lives of the fish they were trying to catch".

Two groups of fishing gear are distinguished: active and passive gear. In contrast to active gear, passive gear has to be searched out by the fish voluntarily. Therefore, passive gear, and particularly the simpler and less complicated types, require a greater knowledge of fish behaviour, so that they can be designed in such a way that fish will not evade them. But also the design of such active gear as trawls, particularly pelagic ones, can be improved as a result of an understanding of fish behaviour (Chapman, 1964). This is especially true for midwater trawls, where the design must be in agreement with the behaviour of the fish to be caught (Mohr, 1964).

The construction of most fishing gear results from practical experience, but despite the antiquity of fishing there is not a single type of gear which could not be improved if more were known about fish behaviour.

The factors which should be taken into account when designing and constructing fishing gear may be divided into the following categories:

(a) selection of material

(b) size and shape of mesh

(c) design of guiding equipment

(d) devices for retaining the catch

Selection of the net material - When Isaac Walton (1653) advised his pupil to try angling with a single hair as he would then catch more fish, he evoked a principle which applies also to modern commercial fisheries. For the lines of amateur anglers, as well as for the nets of commercial fishermen, the finest possible material always gives the best catching results: the reasons for this are that the visibility and the reflection of current diminishes in relation to the diameter of the material. The desire for fineness, however, sometimes conflicts with the demand for strength and elasticity, a favourable characteristic for one factor might be outweighed by an unfavourable characteristic for one of the others; e.g., greater strengths of synthetic fibres can often be achieved only at the expense of elasticity, and vice versa. Thus the following factors have to be considered when selecting net material:

(a) strength

(b) visibility

(c) filtration

(d) elasticity

Strength - Little is known about the strength that fish can develop to liberate themselves from fishing gear. Predacious fishes can bite the line and, to prevent this, hooks with long shanks are used, or stronger materials are fitted between the hook and the line; these sometimes consist of wire or, in shark fisheries, of heavy chains. Besides their ability to bite through the lines or nets, the actual weight of fish or the effect of their struggles as they are being hauled in must also be considered.

The greater thickness of material with a wanted strength which is needed in nets made of natural fibres, hampers their efficiency, but such material is nowadays rapidly being replaced by finer synthetic materials of equal strength and this allows fishing gear to be designed which takes advantage of increasing knowledge of fish behaviour.

Visibility - The visibility, or rather the invisibility, of fishing gear is particularly important in such passive gear as gill nets and tangle-nets. The superiority of transparent polyamide monofilament in such nets depends on the fact that the colour of the netting is less important than is its contrast to the surroundings. Therefore, the success of different coloured nets depends on the type of water and the season and many fishermen use gill nets in different colours in the hope that one of them will yield good results. Monofilament gill nets of low visibility catch much more fish than the now almost obsolete cotton nets, and they have occasionally revealed the existence of a species which was previously unknown in certain waters. Such nets are now widely used and in some cases they have resulted in the obsolescence of previous fishing methods, e.g., the beach seine fishery in Germany has now been replaced by a gill net fishery which is less expensive to operate. In Madagascar, the fishery "à la tente" for jumping fish has given way to monofilament gill nets which do not cause the fish to jump. The visibility of polyamide monofilament gill nets gradually dim with age and it is probable that their efficiency diminishes (Katanyuwong, 1967).

In line fishing, the importance of the invisibility has resulted in a rapid adoption of polyamide monofilament especially for branch lines in place of their previous ones of cat gut and silk. The visibility of a netting influences the behaviour of fish, also in other types of gear. It is well known that fishes keep a certain distance away from a moving net as it approaches, in the same manner as from the netting of a stationary pound net. By means of "netzonde" this habit has been observed in connection with midwater trawling for herring (Schärfe, 1960; Mohr, 1964 a). The distance which they keep depends on the density of the school, its physiological condition and possibly also on the towing speed. When fish keep several metres away from the netting the effective opening of the trawl is reduced. This has been successfully compensated for by designing trawls which have particularly large openings (Schärfe, 1966 b). The opening height for pelagic herring nets has been increased over the last few years from 10 to more than 30 metres as a result of these observations. Visual and tactile stimuli may be responsible for this fish behaviour.

Filtration - Fishes can probably sense minute changes in water pressure caused by the pressure build-up in front of an advancing net.

With active gear like trawls or seine nets filtration is made as good as possible by using large meshes in the anterior part of the gear which allows the water to pass freely through it. The same applies to traps, stownets and to a certain extent also for lift nets. With the passive gill nets the water blockage caused by a cross current is kept to a minimum by using yarns of the smallest possible diameter and with the greatest softness. The degree of relaxation of a gill net hanging in the water is partly achieved by having only a slight tension between the cork line and lead line or by hanging the net with plenty of slack. Experiments have revealed that for the efficiency of gill nets, visibility is more important than softness of the yarns, but that with nets of equal visibility, those with the least stiffness catch more fish (Mohr, 1965 b).

Elasticity is an important factor in gill nets, where a too high elasticity is undesirable. This is considered the reason why gill nets made of flax or man-made polyester fibres can have a higher efficiency. Riedel, (1963), points out that not only the qualities of the net yarn are important, but the "elasticity of fish's flesh, which is in relation to its physical condition and the fish's swimming power against an obstacle". Net yarns should permit fish to penetrate the meshes of gill nets easily. Exceedingly fine yarns cut into the fishes. Therefore, for herring gill nets the diameter of netting yarn should not be less than 1 mm even though the strength of such material is much higher than necessary.

5.1 Selection of netting

The same factors as mentioned for the choice of net material are also important for the choice of netting, including mesh size and mesh shape.

Mesh size - It has been proved and documented in a film on seine netting for flatfish in Scotland that fish can escape through a mesh size which is actually less than their own girth. With many fishing gear, especially tangle nets and some gill nets, the mesh size is not in relation to the size of the body of the fish, as such nets often catch much larger fish, not by gilling them, but rather by entangling them as they attempt to escape. On the other hand, in some fishing gear, like trawls, fish do not escape through large meshes.

Shape of meshes and hanging - Recent investigations have revealed the importance of the shape of the mesh. Selection experiments with trawls having codends with rigid square meshes gave a different result from those with soft diamond-shaped netting (Clark and Fritz, 1957; v. Brandt, 1958).

Experiments with gill nets have shown the importance of the shape of the mesh (Riedel, 1963; Mohr 1965 a). The hanging ratio is influencing the mesh shape. For *Tilapia* the hanging ratio is of decisive importance for the efficiency of the gill net, but for roaches, different hanging ratios had no effect on the catches; the mesh size alone was decisive. For catching herring the mesh size is also decisive, but herring fishing is aimed at a limited size-group. The catches of fishes with fins and spines in gill nets generally depend upon the hanging ratio: owing to evading movements, some fishes become entangled more easily in loosely-hung netting. In general, nets hung with greater slack catch larger fish.

5.2 Guides

Some fishing gear incorporate equipment to guide the fishes from a rather far distance into the opening of the fishing gear or the catching chamber. Trap nets of all types as well as otter board stownets operated in the rivers of Central and Western Europe are examples of fishing gear with stationary guides. The wings of trawls of seine nets can be classified as mobile guides. Both types have been investigated, in particular the mobile guides, as they not only guide but also achieve a herding effect.

Stationary guides - The effective catching range of traps is increased by having guiding fences leading to their opening, thus leading fish into their catching chambers. Such guides are detected by the fish, either optically or by their tactile senses, or by the reflection of the movement of water (damming-phenomena; Chapman, 1964). It has proved that this phenomenon can also be attained by alternating rows of bamboo sticks fixed in the bottom. The fishes could easily swim through such a guiding weir, and they would also do this if they were frightened, but experience has revealed that the swinging sticks suffice to keep the fishes at a distance from the guide and to lead them along it. This practice is used in Thailand in connection with fish weirs, as well as in Northern Europe where some guides of the Danish pound nets consist of twines loosely stretched between an upper and lower line, enough to discourage fish from swimming through. Fishes cannot be guided indefinitely along such fences. If the guides are too long the fish may turn away. Some fishes try to jump over the guides and in this case the guide should be higher than the surface of the water.

If guides do not begin from the bank or shore the fish may be guided in the wrong direction. To prevent this, certain guides end in a large-diameter curve (Foderá, 1964). Examples of this are found in tuna weirs (*tonnara*) of the Mediterranean and off the Atlantic coast. Sarà (1967) demonstrated strikingly how tuna can be guided by more than one bend in the guiding net in the opening of the trap. Fish swimming along the guide follow this bend and are thus brought to a circular or elliptic course. As fish do not swim around sharp corners, it is necessary that the "bend" should not have a sharp angle, but be shaped like a bow.

This technique of guiding fish from a straight, to an elliptic course, is also utilized in some purse seine fisheries, especially those operated on the one-boat system. When hauling the purse seine, the vessel is partly drawn into the net, thus developing pockets at the bow and stern. These compel the fish circulating inside the net to reverse. If this was not done the fish would swim directly towards the open space between the two net-ends and escape.

Mobile guides - Large mesh wings on each end of gear such as trawls and seine nets herd or concentrate fish into the centre of the net which has a smaller mesh which the fish cannot penetrate. Such an effect is also achieved by the legs and sweep lines between otter boards and trawl nets. Kites attached to secondary headlines above a trawl act in the same manner, i.e., they drive fish down and into the range of the trawl mouth. These kites therefore extend beyond the effective range of a 4-metre opening trawl to as much as 14 metres above the bottom.

It has not yet been explained if such guiding devices depend on the visibility of the gear only, or whether other stimuli, such as pressure waves have some effect.

Fish which have a habit of escaping over the top of the net may be prevented from doing so by having the top of the net made in the form of a roof. With pelagic trawls the lower part of the net is sometimes extended to prevent escape under the net. The same shape, somewhat like a dust-pan, is sometimes used for drive-in-nets, and to a lesser extent, both forms are found in some types of fyke-nets.

Observations made under water have revealed that fish can be guided into a towed funnel-like net without them making a serious attempt to escape, even though the meshsize would allow them to do so. In places where a trawl net bulges, eddies are created and the normal free flow of water is disturbed. It is through such places that fish usually try to escape and these places can be recognised by the presence of meshed fish. To find and to overcome such irregular shaped parts of a net which affect the smooth flow of water and encourage fish to escape is, therefore, of paramount importance to the net-maker. Direct underwater observations of either a full size or a scale model trawl in action is the best way of detecting such trouble spots (Schärfe, 1966 a).

5.3 Non-return devices

Scoop nets, which move rapidly through the water, do not require special devices to prevent fish from escaping. The same applies to such gear as tubular traps and certain nets which operate on the principle of fish being carried into them and held there by the force of the current. But with most types of gear even when dragged, fish would be able to escape from the net unless certain arrangements were made to hinder or prevent fish from finding the net opening. Most types of traps, stownets, trawls and seine nets incorporate such non-return devices. Cast nets and certain types of net walls which are used in the Far East also have special devices in the form of retaining pockets, which, by exploiting the behaviour of the fish to be caught, prevent their escape. These non-return devices fall into the following categories:

(a) steps

(b) slits and funnels

(c) retaining pockets

Steps - Many pound nets and traps in the Mediterranean and in Japan are fitted with a non-return device which may be likened to a ramp. The lower end begins on the sea-bed and the ramp rises gradually, guiding fish over the highest point and into the catching chamber. Once inside the trap, fish usually return to deeper water and are unable to escape. An excellent example of the practical application of fish behaviour in the design of fishing gear (Kajewski, 1959; N.N., 1960).

Slits and funnels - Slit or funnel-shaped entrances are commonly used in may types of fishing gear, including trawls, seine nets and traps. In some cases, the inner end of the entrance is provided with spikes or spines, preventing the fish from returning. The end of the funnel is often protruded like a cone. Fish, once inside the net or trap then follow the walls of the gear in their attempts to escape. Unable to turn sharply they are thus guided away from the opening of the cone.

Pockets - Small pockets are fitted to certain types of gear. Many cast nets have pockets near their perimeter in which fish are trapped as they attempt to escape. In the Far East, certain net walls have pockets at their lower edge to catch fish and crayfish which attempt to escape beneath the net (Chen Chi Tang, 1960).

Pockets are also used on the upper edge of some fishing gear, particularly to catch shrimp, which usually move upwards in their attempts to escape. This habit of shrimp led to the design of a type of beam trawl in which the interior part was divided in two by a horizontal wall. Shrimp were thus guided into the upper codend made of small meshes, while flatfish could escape from large meshes in the lower codend (Boddecke, 1965). Shrimp can escape in front of a slow-moving beam trawl and Japanese fishermen therefore use retaining pockets at the upper edge of such nets.

6 CONCLUSIONS AND GAPS IN OUR KNOWLEDGE

Attempts are now made in the various fisheries to consider fish behaviour in the development of fishing methods and tactics and in the construction of fishing gear. Discussions at the Fishing Boat Congress in Götenborg (1965), revealed that fish behaviour is also beginning to be considered in the design and construction of fishing vessels, e.g., improved engine installations in herring and tuna vessels to reduce noise.

Primitive fisheries often seem to apply knowledge of fish behaviour more than in the highly developed industrial fisheries. Original fishing methods are operated with a maximum of knowledge of the behaviour and a minimum of gear. Modern industrial fisheries try to compensate for a lack of knowledge of fish behaviour with a maximum of sophisticated technical arrangements.

Gathering knowledge of fish behaviour, either by direct observation or by experiments, would improve old fishing methods and find new ones (up to now the only new examples are electrical fishing and pump-fishing). We must learn from behaviour studies to increase the efficiency of a fishing method not only by improving gear construction and gear operation but also by influencing the fish behaviour in a way that will result in improved catches and remove fisheries, as much as possible, from the sphere of accidental success.

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R/9

METHODS AND TECHNIQUES FOR STUDYING FISH BEHAVIOUR IN THEIR NATURAL ENVIRONMENT

by

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Abstract

Various methods and techniques for studying fish behaviour in their natural environment are reviewed. Examples are given of aqualung surveys of artificial fishing reefs, special applications of underwater television and observations from submarines and other submersibles. The bathysphere, KUROSHIO, and a proposed new Japanese research submarine are described.

METHODES ET TECHNIQUES POUR L'ETUDE DU COMPORTEMENT DU POISSON DANS SON MILIEU

Résumé

L'auteur passe en revue diverses méthodes et techniques pour l'étude du comportement des poissons dans leur milieu naturel. Il fournit des exemples d'observation de récifs artificiels au moyen de scaphandres autonomes, d'applications particulières de la télévision sous-marine, et d'observations faites à partir d'engins sous-marins. L'auteur décrit la bathysphère "Kuroshio", ainsi qu'un projet de nouveau sous-marin de recherche japonais.

METODOS Y TECNICAS PARA ESTUDIAR EL COMPORTAMIENTO DE LOS PECES EN SU AMBIENTE NATURAL

Extracto

Se examinan varios métodos y técnicas para estudiar el comportamiento de los peces en su ambiente natural. Se dan ejemplos de estudios de arrecifes pesqueros artificiales, aplicaciones especiales de televisión submarina y observaciones desde submarinos y otros sumergibles. Se describen la batisfera KUROSHIO y un nuevo submarino japonés para realizar investigaciones submarinas.

1 INTRODUCTION

Methods and techniques for studying fish behaviour in their natural environment have been advanced in recent years through the development of aqualungs, diving chambers, towed submersibles, submarines, cameras, T.V. etc. Much of this development has been stimulated by a world-wide trend to intensify exploration and exploitation of ocean resources. To accomplish these objectives man must have access to the ocean depths; to witness actual conditions, conduct various investigations and obtain needed samples. Japan, a country lacking natural land resources, considers underwater studies of the continental shelves and their environments to be of vital importance.

Examples of the use of submersibles and other underwater observational techniques in the study of fish behaviour are given below.

2 AQUALUNG STUDIES ON ARTIFICIAL FISHING REEFS

Many artificial fishing reefs have been placed in the sea around our country in attempts to attract fish populations. Observations have been made on the attraction of fish to the reefs by aqualung surveys (Fig. 1 and 2) and also by echo-sounding and fishing experiments. However, very few experimental studies on the behaviour of fish to shape and size of the underwater structures have been conducted.

Ogawa (1965, 1967) has given special attention to fish behaviour in relation to the size of artificial reefs and obtained interesting results. Using croakers of 10 to 20 cm length he has shown that attraction to the reef depends on the size of the structure rather than other factors such as food, shadows, etc. Other researches have obtained fragmentary results on the reactions of fish to reef but much more work needs to be done. The present author has begun studies on the relation between underwater polarization of sunlight and effectiveness of artificial reefs. Further investigations will depend heavily on the use of aqualungs.

3 THE BATHYSPHERE, KUROSHIO

Inoue *et al.*, (1961) described the construction of the bathysphere, KUROSHIO, which can be suspended from a mother ship to a depth of 200 m. The bathysphere was completed in 1951 for investigations on the ecology and behaviour of fish and other marine organisms, surveys of fishing grounds and observations on fishing gear in actual operation. KUROSHIO has made a few hundred dives in various places around Japan with excellent results. In 1960 the bathysphere was converted from a suspended type to a free-submerging unit, although power is still supplied by the mother ship. KUROSHIO is still operational and has been used in recent studies on scallops, abalone, croakers and fishing ground assessment (Tamura, 1963; Inoue, 1964).

4 A PROPOSED NEW JAPANESE RESEARCH SUBMARINE

In order to extend the scope of research over the continental shelf to the continental slope we are constructing a new research submarine which can dive to depths of 600 m. The order for this submersible has been given to the Kawasaki Dockyard which has abundant experience in building submarines and is renown throughout the world for its superior techniques in this field. Principal specifications, equipment and capabilities of the new vessel are given in Table I.

A significant feature of the new vessel will be its operational depth of 600 m which considerably exceeds the 300 m depth of most conventional research submarines. The pressure hull will be of spherical construction rather than the conventional cylindrical construction which will reduce weight and accommodate more equipment. A propulsion system driven by an oil-dipped battery will be housed in a nonpressurized compartment to save internal pressurized space for other purposes and eliminate the hazard of battery gas. The ship will not have a rudder as all movements will be directed by the propellers.

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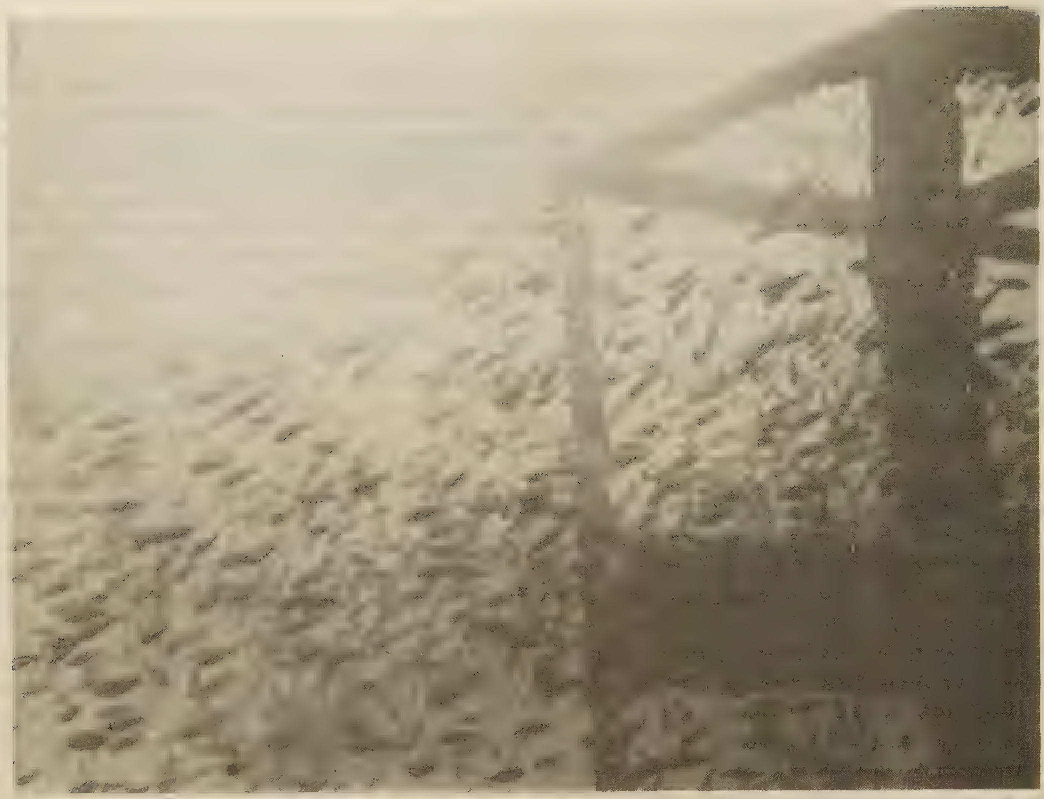

Fig. 1 Japanese grunt gathering around an iron frame artificial fishing reef at a depth of 30 m in Ajiro Bay, Shizuoka Prefecture.

Fig. 2 Cardinalfish gathering around a concrete block fishing reef at a depth of 30 m in Ajiro Bay.

TABLE I

Principal specifications, equipment and capabilities of a proposed new Japanese research submarine

Expected Completion Date: December 1968

Dimensions and performances:

a.	Length	about	15.3	m
b.	Width	"	5.5	m
c.	Depth up to Deck	"	5.0	m
d.	Draft	"	4.0	m
e.	Displacement (submerged condition)	"	85	tons
f.	Depth for safety submerging	"	600	m
g.	Complement	4 (Including 2 researchers)		
h.	Speed, submerged	about	3.5	knots
i.	Speed, surface	"	3.5	knots

j. Continuous operation hours and distances

Submerged: 3 hours, 10.5 sea miles at 3.5 knots

On the surface: 10 hours, 15 sea miles at 1.5 knots

k. Power source: Oil dipped battery

l. Main Propulsion:

One set of nozzle type propeller driven by submersible 11 K.W. motor

m. Auxiliary Propulsion:

Two sets of nozzle type propellers driven by submersible 2.2 K.W. motors

Equipment:

a. Plankton Sampler
b. Manipulator
c. Reversing Water Bottle
d. Bottom Sampler
e. Underwater Television
f. Seismic Profiling System
g. Heat flow meter
h. Depth Sound Speed Measurement Set
i. Sea Bottom Current meter
j. Salinometer
k. Water Temperature meter
l. Ocean Magnetic meter
m. Gravity meter
n. Deep-sea cameras 1) Movie 1
2) Stereo 1
o. Transparency meter
p. Radiation meter
q. Tape-recorder

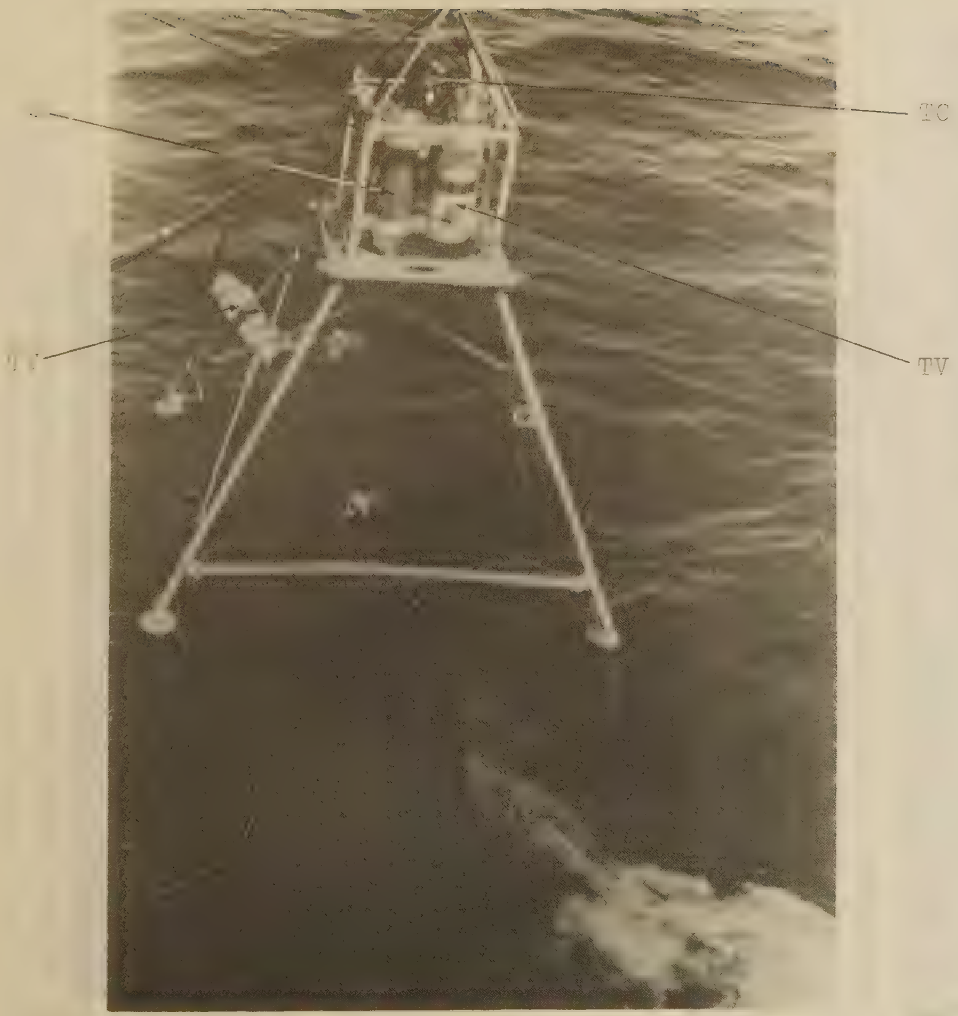

Fig. 3 An underwater television combined with ultrasonic distance meter (Minoru Nishimura)
TC – Transducer and underwater camera
TV – Underwater television, S – Strobe

Fig. 4 King crab at a depth of 70 m off the west coast of Kamchatka Peninsula

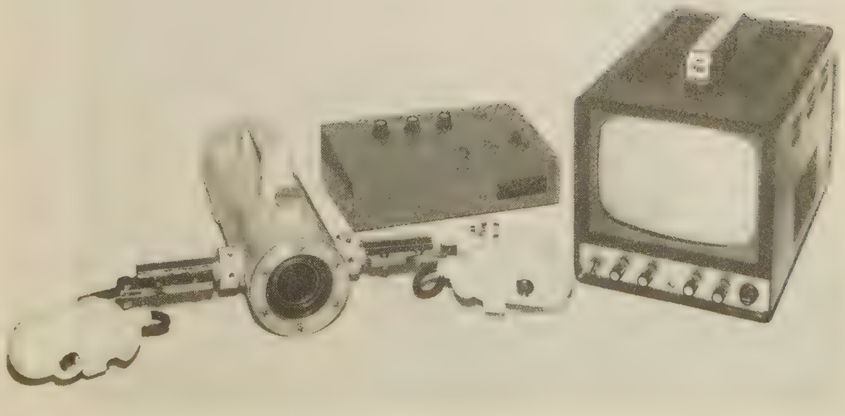

Fig. 5 A small underwater television made in Japan for depths of 200 m

5 OTHER SUBMERSIBLES

Many research submersibles are now in operation by other nations and some have been used for fish behaviour studies. The research submarine, SEVERYANKA, of the U.S.S.R., with an operational depth of about 200 m, has been used to observe the responses of herring schools to shape and colour of trawls (Anon., 1964). Another Soviet submersible (ATLANT-1) of the towed type has appeared and is now carrying out similar investigations on trawling (Anon., 1965a, 1965 b). The ATLANT-2 is believed to be under construction.

In 1966 a small research submarine was built in France (ANOREP-01) for oil prospecting and investigating the bottoms of harbours but it may be considered for studies on fish behaviour as related to fishing techniques and tactics. It is well known that BATHYSCAPHE F.N.R.S.-3 and ARCHIMEDE have made a hundred or so successful dives into great depths and have obtained much valuable data on fish behaviour and other oceanographic phenomenon.

A small research submarine was developed in West Germany to study gear related fish behaviour. In addition to the bathyscaphe, TRIESTE, a number of new research submarines have appeared in the U.S.A. and are engaged in extensive investigations including the subject of this paper.

6 UNDERWATER CAMERAS AND TELEVISION

In Japan underwater cameras began to be studied in about 1955 (Sasaki, 1955) and now are utilized in various fish behaviour studies. Numerous types of portable cameras for divers and deep sea cameras of the suspended variety are used. The state of underwater camera development in other countries is similar to that in Japan.

Underwater television cameras (U.T.V.) are now used extensively. The present author imported a U.T.V. from the U.S.A. to investigate the ecology of individual fish and fish schools, artificial fishing reefs and fish behaviour to fishing gear (Susaki, 1955, 1956). Studies on U.T.V. itself and fish behaviour using U.T.V. have developed rapidly.

Nishimura (1964) constructed an experimental U.T.V. equipped with an ultrasonic distance meter (Fig. 3). The system was developed so that distances from the camera to an object could be measured. In addition, the size of the object, such as a fish, can be determined. By combining an underwater compass with the unit, the orientation of the camera is indicated in the corner at the receiver. The system has been used to study croakers, sea anemones, Ark shells, King crabs (Fig. 4) and others.

Ishida (1963) used U.T.V. to measure the catch ratio of salmon in drift nets. He also observed how salmon were caught in the net and what numbers escaped or fell off while the net was fishing (Ishida, 1967).

At present there are several U.T.V. manufactures in Japan (Fig. 5) and their use is becoming more popular in artificial fishing reef and sea bottom studies, of course in other countries such as the U.S.A., England, Scotland, France and the U.S.S.R., U.T.V. is also frequently used in fish behaviour studies (Barnes, 1962).

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REVIEW OF INFORMATION ON THE BEHAVIOUR OF GADOID FISH

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Abstract

The available information on the behaviour of gadoid fish of greatest commercial importance: cod, haddock, coalfish, hake and whiting is reviewed. Both patterns of general behaviour: migrations, vertical movements, schooling, feeding and spawning behaviour, as well as reactions to fishing gear and tactics are covered. Considerable information is at hand on distribution and horizontal and vertical migrations, but less on schooling, feeding and spawning behaviour. As regards reactions to fishing gear, evidence of response to visual, mechanical and chemical stimuli are discussed.

ANALYSE DES RENSEIGNEMENTS DISPONIBLES SUR LE COMPORTEMENT DES GADIDES

Résumé

L'auteur passe en revue les données disponibles touchant le comportement des gadidés présentant le plus d'importance sur le plan commercial: morue, églefin, lieu noir, merlu et merlan. Il étudie à la fois les comportements généraux (migrations, mouvements verticaux, formation de bancs, alimentation, reproduction) et les réactions aux engins et tactiques de pêche. S'il existe d'amples renseignements concernant la répartition et les migrations horizontales et verticales, on est moins bien renseigné sur le comportement en matière de rassemblement en bancs, d'alimentation et de reproduction. Pour ce qui est des réactions devant les engins de pêche, l'auteur examine des indices révélant l'existence d'une réponse aux stimuli visuels, mécaniques et chimiques.

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EXAMEN DE LA INFORMACION SOBRE EL COMPORTAMIENTO DE LOS GADIDOS

Extracto

Se examina la información existente sobre el comportamiento de los gádidos de mayor importancia comercial: bacalao, eglefino, colín, merluza y merlán. El estudio se ocupa de ambas clases de comportamiento: migraciones, movimientos verticales, agrupamiento en cardúmenes, alimentación y desove; y reacciones ante los artes de pesca y las tácticas pesqueras. Se dispone de abundante información sobre la distribución y las migraciones horizontales y verticales, pero en menor cantidad sobre los hábitos de gregarismo, alimentación y desove. Por lo que se refiere a las reacciones a los artes de pesca, se examinan las pruebas que se poseen de su respuesta a los estímulos visuales, mecánicos y químicos.

1 INTRODUCTION

The foremost and keenest observer of fish behaviour has always been the fisherman, since this subject really forms a part of the fisheries themselves. We should therefore expect that for gadoid fish which have been exploited systematically through hundreds of years a great deal of knowledge on the behaviour of the various species had by now been accumulated in this way. In a sense, this is indeed true: without the experience gained through generations on the ways of the fish in the sea, proper fisheries could not have existed prior to our technological era. Most of this knowledge is, however, inaccessible to a literature survey and it is also often of limited value for a full understanding of the behaviour of fish. This is so because conditions of "controlled experiments" are generally absent in the fisherman's observations. Negative results and observations may be interpreted in any likely or unlikely way. Absence of fish from the usual grounds or failure of fish to be caught on passive gears were especially in former times explained as being the effect of a change of the behaviour of the fish caused by any rational or irrational powers. New fishing techniques have often been blamed for disturbing the normal ways of fish as have been engines, motors and echo sounders. Some of these cases tell us perhaps more about the psychology and behaviour of the fisherman than about the fish. But one may also well argue that the fact that a modern fishing vessel with all its propeller, engine and gear noises does not scare the fish out of reach of the gears is perhaps a demonstration of the adaptability of the fish in its bebaviour rather than of lack of original reaction to the stimuli. In the formulation of problems and programs of fish behaviour studies one is no doubt wise in drawing on the experience and knowledge of the fisherman.

It is of course the general inaccessability of fish in their natural environment to direct human observations that has prevented the development of systematic fish behaviour studies up to our times, when it has finally been made possible through the techniques of acoustic instruments, underwater photography and television, diving and large scale aquaria experiments. Only the last 15 years or so have seen any substantial progress in this field.

This review will cover only the gadoid species of greatest commercial importance: cod, haddock, coalfish, hake and whiting. There is a considerable degree of similarity among these species in many important aspects of their behaviour and the review has been made by subject matter rather than by species groups. Special reference will be made to observations of differences of behaviour between species.

Although it is assumed that the focus of interest of the conference will be on the reactions of fish to fishing gear and techniques, it was found useful to review briefly also the knowledge on the general behaviour of these fish, especially as regards their migrations, vertical movements, and schooling, feeding and spawning behaviour.

2 PATTERNS OF GENERAL BEHAVIOUR

A great deal of information is available on the various aspects of the "normal" behaviour of gadoids in their natural undisturbed environment. The distribution of the species have been related to various environmental factors. The often large-ranging migrations and displacements have been described and a number of observations covering vertical movements are available. We seem, however, to know considerably less on the schooling, feeding and spawning habits of these fish, which is unfortunate since these subjects are of special importance for various types of fishing techniques.

2.1 Environmental characteristics affecting the distribution of the fish

This subject was treated extensively at the ICNAF Environmental Symposium in 1964 where most of the contributions dealt with gadoid fish (see ICNAF Special Publ. No.6) and it will only be dealt with very briefly here.

Sea temperature has, in most cases, been used as the physical factor of the environment with which to compare biological data, but as pointed out by Lee (1964), this may be a shortcut since the true interrelationship may be a complex one and involve a number of other factors. Temperature is conveniently and easily observed and it has been successfully used as a guide in fish surveys as by Midttun (1964), and also directly, by fishermen to indicate likelihood of presence or absence of fish on the grounds.

There is no doubt a need for more information on the direct effects on fish behaviour and physiology of changes in the various physical and chemical factors of the environment. For the Barents Sea cod Woodhead and Woodhead (1959), found that fish sampled from waters of very low temperatures were in a state of osmotic imbalance, having a high blood salt content. The physiological limiting temperature for this imbalance was higher (2° C) from October till June than during the rest of the year (0° C). This coincides with observations referred to by Lee (1952) and others that paying quantities of cod in this area are rarely taken in temperatures of less than about 2° C except in summer when heavy fishing may sometimes occur in waters of 0° C or even slightly lower. Physiological studies of this type can no doubt lead to a much better understanding of the relationship between fish behaviour and the physical and chemical environment.

2.2 Migrations

The most conspicuous long-distance migrations of gadoids seem to occur in the stocks which occupy the northernmost limits of the distribution areas of the species, e.g.Arctic and Greenland cod, Arctic haddock and Norwegian coalfish. The distances covered for these stocks on their spawning migrations regularly range up to a thousand nautical miles and more. Recently, extensive migrations have been demonstrated also in the hake stocks of the Western Pacific by Alverson, (1967) and Chile by Saetersdal and Villegas (1967) Whereas most spawning migrations are contranatant resulting in a passive drift and spreading of the off-spring by surface currents over the area of distribution of the stocks, the hake migrations referred to above were denatant. The North Pacific hake moves south and downstream to spawn and the Chilean hake moves north and downstream. In both of these areas, however, a sub-surface counter-current probably exists which may act as the transporting agent for the eggs and larva.

Jones (1964) discussed the relationship between water currents and migrations. He found that although the spawning grounds are often located up-stream relative to the area of distribution of the fish, this does not necessarily mean that the spawning migrations actually occur against the currents since fish may move in gyrals always downstream or be transported by sub-surface counter-currents. Quoting Sund (1932), he thus thinks it likely that the arctic cod may be brought to Lofoten by such a counter-current. Recent echo-surveys of the migrating cod in this area cf. Saetersdal and Hylen, (1959) have, however, shown that the cod does not move in the off-shore counter-current as thought by Sund, but along the edge of the shelf and over the shelf itself where the main current component is northwards. With regard to the reaction of fish to water currents, Jones reports that experimental laboratory work has shown that fish will only react when they can detect their displacement through visual or tactile clues. It seems indeed doubtful whether water currents can be a guide in the orientation of migrating fish, unless fish can perceive the changes in the magnetic field of the earth set up by the currents as suggested by Royce and others for Pacific salmon (personal communication). The mechanism of orientation is, however, still not understood. In salmon, chemical sensing seems to play an important part in their orientation during the last part of the migrations in coastal waters and rivers and this type of sensing may also be important in gadoids.

Woodhead (1959) has made an interesting observation on the relationship between the physiology of the Arctic cod and its migrational cycle. During the latter (September to March), the thyroid gland was found to be active both in mature and immature fish and it is suggested that thyroid activity may initiate and sustain the active migrations of immature fish during this season (dummy runs), although not as extensive as those of immature fish.

A number of old and famous fisheries for gadoid species have been based on the regular seasonal appearance of the fish in particular localities such as cod in Lofoten and at Iceland and the cod and haddock at the Finnmark coast. Irregularities in the migrational patterns do, however, occur, cf. Saetersdal and Hylen, (1964) and especially in old times these could have drastic effects on the yields of the fisheries. Olsen (1954) has shown that changes in the migrational pattern of the Norwegian coalfish stock sometimes take place and may result in a considerable loss to the stock of big mature fish.

2.3 Vertical movements

Gadoids are commonly classified as demersal fish. This term derives, however, from the times when the evidence of their vertical distribution was the fact that they were principally fished by bottom gears. Later observations especially by echo sounders have, however, demonstrated that the gadoid fish spend a considerable part of their time in mid-water. It would thus be more correct to classify these fish as semi-pelagic. There is often both a seasonal and a diurnal fluctuation in the vertical distribution of the gadoids.

2.3.1 Seasonal vertical migrations For nearly all the species there seems to be the general rule to occupy shallower water in summer than in winter. For the cod in the Bear Island area (Arctic cod), Trout (1957) was able to demonstrate a clear annual cycle of this type from the records of depth of trawl fishing. Iversen (1934) reports that in West Spitsbergen in summer the cod may be found at only a few meters of depth close inshore.

McCracken (1963) found from an analysis of the fishery that the haddock off Nova Scotia are distributed at greater depth in winter than during the summer months. In the southern Barents Sea, Arctic haddock is regularly caught on float and hand lines in late summer and it may sometimes even be caught in purse seine sets at this time of the year on the Finmark coast. There is a large-scale purse seine fishery for coalfish in summer in the waters of North Norway.

The seasonal cycle in the depth distribution of hake, shallow in summer and deep in winter, is well known and has been described for the North European hake by Hickling (1935), for the North Pacific hake by Alverson (1967) and for the South Pacific hake by Saetersdal and Villegas (1967,2).

Brunel (1965) suggests that seasonal changes in the vertical distribution in cod may be a response to availability of food organisms. No doubt it may sometimes also be a response to changes in the physical/chemical environment or related to spawning cycles.

2.3.2 Diurnal vertical migrations Diurnal patterns in the vertical movements of gadoids have been observed in a great number of studies. Based on an analysis of trawl catches Trout, (1957) concluded that the Bear Island cod lifted off the bottom during the hours of darkness. Konstantinov (1964) made a similar analysis of cod and haddock catches in the Barents Sea by bottom trawl and found that during autumn and spring there was a clear diurnal variation with higher catches during the day, but in winter and summer when there is little variation in daylight, catches were about the same. Additional evidence from echo sounder observations proved this to be the effects of diurnal vertical migrations when light conditions changed by day and by night. Woodhead, (1964;2), from an analysis of research vessel catches by trawl of Arctic cod and haddock during winter found little difference between day and night catches for cod, but dawn and dusk hauls were 125 per cent and 141 per cent of day catches respectively. Night catches of haddock were 35 per cent of day catches.

One should of course note that the fishing power of a trawl may vary at different times of the day, (this will be discussed below) and that all diurnal variations in catch should not necessarily be ascribed to vertical migrations.

Beamish (1966) observed the vertical distribution of cod and haddock from Nova Scotia and the Gulf of St Lawrence by echo sounders and found that both species were usually closely associated with bottom during the day, but moved off after dark and dispersed in midwater. Cod did not always return to the sea bed by day, but the haddock was more "demersal". The catches in bottom trawls varied in accordance with this pattern and were generally lower by night. Brunel (1965) found two types of vertical migrations of cod in the western Gulf of St Lawrence: the "classical" nocturnal type bringing cod up into midwater from mid July to fall and a residual type observed from May till mid July, bringing more, or as many, cod in midwater during the day apparently in response to pelagic swarming prey. Jones (1956) found that from October till end April better catches of haddock are usually made at night at Faroe and he thinks that this is due to a tendency during daytime for large haddock to leave the bottom.

Schmidt (1952) found a marked diurnal variation in bottom trawl catches of coalfish for the whole of the north-east Atlantic waters and from the additional evidence of echo sounder observations he describes this as an effect of vertical migrations. He furthermore found a size-selection in the vertical movements: small and middle sized fish were in relatively higher proportion on the bottom during darkness while big coalfish principally pelagic at night would descend to the bottom at dawn and replace the now ascending small fish. Wagner (1959) found a somewhat similar change of size-composition of catches of coalfish with predominance of big fish during the day and small fish in the morning and evening.

A number of observations are available on vertical diurnal movements of hakes. Hickling (1935) states that the North European hake is a midwater feeder at night and "lies quietly on or near the sea bed during the day". A bottom trawl will only catch hake in much diminished quantities during the night, whereas the old-time fishermen who caught hake on hand lines did so in mid water at night. Zupanovic (1967) says that the highest catches of Mediterranean hake are obtained mainly in the first haul after sunrise, and the catch then gradually decreases as the day progresses. Alverson (1967) observed that the schools of North Pacific hake which during daylight lie just off or in contact with the sea bed would rise at night and disperse in midwater. Vestnes et al. (1965) found that the hake in Chile have the regular habit of lifting off the bottom and spreading out in thin layers during night time. The findings of the last two references were based on extensive echo sounder records.

Blaxter and Parrish (1958) studied diurnal movements of whiting in Loch Striven and found that this fish would adjust its depth distribution during the day in accordance with the prevailing light conditions. At night juvenile whitings would rise towards the surface. Woodhead (1964, 1) says that shoals of North Sea whiting have been observed to rise at dusk and disperse singly throughout the water column. Bagenal (1958) found that daylight catches of haddock, cod and whiting in a bottom trawl were consistently higher than night catches.

2.4 Schooling behaviour

With the probable exception of the coalfish, gadoids do not form the type of well-defined uniformly packed schools so well known from clupeoids and tunas. During spawning the cod in Lofoten aggregate in irregular schools or in a layer in midwater during the day; these, however, break up during darkness hours into a much thinner uniform layer cf. Saetersdal and Hylen (1959). This night distribution can hardly be defined as a school, since the fish seem to be distributed randomly and thinly rather than in any regular manner. Ellis (1956) observed the behaviour of cod occurring in midwater over a trawling ground in the Barents Sea, and found that the discrete schools recorded in daylight dissolved into a "single-fish" layer during hours of darkness. That vision must be one of the most important factors governing school formation was also shown by Blaxter and Parrish (1958) for whiting. This species aggregated during darkness at a distance from an artificial light source. The records presented by Schmidt (1957) of coalfish from Icelandic waters also show very clearly how the schools of this species change into a continuous pelagic "fish layer" during the night. For North Pacific hake, Alverson (1967) describes the schools during daytime as long narrow bands from several hundred meters to 20 km in length and 0.5 to 3 km in width. In the vertical plan the schools are from 6 to 20 m deep. At night the schools rise and disperse. Vestnes et al. (1965)found a very similar schooling behaviour in Chilean hake with irregular and partly broken up bands of fish aggregations during the day and thin swarms dispersed throughout the water column at night. In an analysis of the effects of light on the behaviour and distribution of demersal fish Woodhead (1964, 1) reports observations of a marked diurnal cycle in the activity of cod in aquaria, with swimming activity several times higher at night than during daytime. This could then be a form of photo-kinesis, but it is suggested that there is probably also an endogenous 24 h cycle of physiological and locomotor activity in many fish. If this is so the gadoids would then be "resting" when in schools during the day, but actively hunting around in midwater for food at night.

2.5 Feeding behaviour

Feeding cycles have been studied on the basis of analysis of stomach contents and catch rates on hand lines. For the Arctic cod Zadulskaja and Smirnov (1939) found that the most intensive feeding occurred during the day as follows: in winter in late afternoon, in spring at midday, and in summer and autumn in the morning. Konstantinov (1958) found on the other hand that the most intensive feeding of Arctic cod and haddock took place during the night. Bratberg and Hylen, (1964) analysing hooking rates on hand lines for Greenland cod, found in one area where the cod were feeding on capelin, that the appetite of the fish (for rubber worms) was highest from early morning till noon. In another area, catches increased from late evening till midnight and then decreased towards early morning. Here the cod was feeding on krill. In one instance, cod was found to be actively feeding at a water temperature of 0.5°C.

By the species composition of the food of the European hake, Hickling (1935) shows that this fish must principally be feeding in midwater where it is usually found at night. Wagner (1959) analysed the stomach contents of coalfish and found that fresh food was particularly frequent at dawn and at dusk. He says, however, that the resulting bimodality of the feeding cycle may be an apparent one only, since it could be brought about by sampling of different parts of the stock.

It thus seems that no definite conclusion can be drawn as yet with regard to a possible diurnal cycle in food intake. Apparently some feeding may take place at any time of the night or day.

Trout (1957) found an annual feeding curve in the Bear Island cod, lower in winter than in summer. During the height of the spawning season, feeding seems to be low in cod. Sundnes (1964) analysed the ways in which the Lofoten cod was caught by the hand line hooks and found that during intensive spawning a great number of fish were hooked in the body or tail, while they were caught by the head or mouth after spawning, indicating a higher interest in food. Rollefsen (1953), from an analysis of the size selection by different fishing gears in Lofoten concluded that of the spawning fish the old and big cod was feeding less heavily than the young and small.

Finally, some interesting observations by Templeman (1964) on this subject should be mentioned. He found that the availability of food was an important factor, causing aggregations of importance for commercial fishing of cod and haddock in the Newfoundland and Labrador areas. Cod concentrations were at times found to feed heavily and almost entirely on portions of cod discarded by trawlers, and this might help to hold schools together or at least make them more related to the bottom. Many fishermen claim that such discards scare the fish away from the grounds.

2.6 Spawning behaviour

Relatively little information is available on the actual spawning behaviour of the gadoids. For most of the stocks there is a seasonal gathering on special well-defined spawning grounds. Already Hjort (1914) was able to chart the spawning locations of the

Arctic cod on the coast of North and Western Norway by plotting the ancient traditional "skrei grounds" or "med" on depth charts. They appeared to fall closely along the 50 fm line. The latest echo sounder observations have shown that the mean depth of the spawning schools of Arctic cod is 50 fm or slightly less. From tank observations Rollefsen (1934) described the spawning act of the cod: after an introductory courting two and two fish - male and female - swam belly against belly while eggs and milt were being whirled together by the vigorous movements of the tail fins. From the relative sex proportions caught in various fishing gear in Lofoten, 60 per cent males in gill nets as against 50 per cent on the unselective purse seine, Rollefsen (1953) concludes that the male cod plays the more active part in the spawning behaviour. Another observation from the Lofoten fishery is that after the arrival of the fish on the grounds, catches by passive gears such as hand lines, long lines and gill nets, may still remain poor for some time because of apparent inactivity of the fish which are said by the fishermen to be "moping". Seemingly both swimming and feeding activity remain at a low level for a period immediately prior to spawning cf. Saetersdal and Hylen, (1959).

For the North Pacific hake, Alverson (1967) describes the spawning schools as different from the ordinary schools of this species. They appear as large continuous bodies of fish increasing in density towards the centre and up to 40 m deep. Pronounced vertical migrations of spawning hake were not observed.

3 REACTIONS TO FISHING GEAR AND TACTICS

Various types of methods have been applied in these studies. Experimental fishing recording catch variations on one or different types of gear have been commonly used, but this method does not always provide the complete control of conditions permitting definite conclusions with regard to the behaviour of the fish. "In situ" observations of fish reactions directly visual in the surface or by divers, or indirectly by photography or television, have given a great deal of important information. Observation by acoustic instruments, although less informative in details, is becoming an increasingly important tool in this work. Finally, observations of basic importance for the understanding of fish behaviour have been made by experiments in aquaria, using the conditioned response technique or simply noting the reactions of fish to various types of stimuli. The latter method is open to an important type of criticism: do fish behave in the same way in aquaria as they would in their natural environment? Sundnes (1957) has made an interesting observation on the physiology of fish in captivity which is of importance for evaluating this question. Studying the oxygen requirements of cod in well boats he found that this was very high immediately after the loading of the boat, and then decreased slowly, indicating a drop in the metabolic rate as the fish were adjusted to their new environmental conditions. In experimental cases in aquaria the oxygen consumption of fish decreased to about half only after 2 to 3 days following a change of site. This demonstrates the degree of care that should be taken to ensure that fish are in a "normal" physiological state before using them in behaviour experiments.

3.1 Response to visual stimuli

In a discussion of this subject, Blaxter and Parrish (1964) conclude that of all the stimuli produced by stationary and moving fishing gears the visual ones are the most important in determining the efficiency of fish capture. There are indeed a considerable number of observations related to the reactions of fish to visual stimuli and they can be classified roughly as follows: comparative trawling experiments, visual and acoustic observations of trawls and other gear in situ and in aquaria and reaction of fish to artificial light and to daylight.

In studies related to trawling gear, the most important question under discussion has perhaps been the identification of the stimuli that produce the herding effect of the mouth of the net and between the bridles. From a series of comparative fishing experiments using trawls with and without the V-D modification, Bagenal (1958) found that the V-D trawl was more efficient both by day and by night. He concluded that in darkness the fish must thus be able to perceive the bridles by the vibrations they set up in the water, and they are in this way scared into the path of the net. In a remark to Bagenal's paper Gulland (1959) points out that the relatively better V-D catches at night could have been caused by a difference in fishing power of the two trawls apart from the V-D modification.

If, however, only vision was involved, the V-D trawl should have been much less effective by night in these experiments than by day and this was apparently not the case. It is also somewhat difficult to accept the idea that the V-D trawl is in general so much less efficient when used in darkness than during daylight. Almost all winter fishing at high latitudes would be similarly affected.

Comparisons of day and night catches cannot contribute much to a solution of this problem since diurnal vertical migrations are common in nearly all of the gadoids. Parrish et al. (1964) think, however, that the higher night catches of such species as whiting and haddock which have been reported from some grounds may be explained as an effect of visual response to the gear resulting in better gear avoidance during the day. In a series of comparative fishing trials studying the effects of reducing the mesh size of the forward parts of the trawl, Dickson (1964) found that this resulted in an increased catch of bigger whiting and haddock. The probable explanation is a difference in avoidance, the bigger and faster swimming fish were apparently able to escape through the square and bunts of the large mesh nets.

Considerable further advances were made in this field following direct "in situ" observations of fish inside and in front of trawls. From a television instrument viewing the cod-end in the aft direction, Livingstone (1962) observed that about 60 per cent of the haddock caught responded to the moving cod-end meshes by keeping pace with the net. Blaxter et al. (1964) describe a series of elaborate studies of the reactions of cod, haddock, whiting and other fish to moving warps and pieces of netting in great tanks, as well as "in situ" observations by underwater photography of the behaviour of fish in front of the groundrope of towed trawls. The aquaria experiments showed that the moving warps and pieces of netting had a herding effect on the fish, but only above a certain threshold of light intensity which roughly corresponds to the light at depths up to about 50 fm in the open sea under average daylight conditions. The distance of reaction was only about 1 to 2 m. Below this threshold of light intensity reaction of the fish to the moving warps and process of netting was much reduced. These findings were confirmed by the results of the photographic observations of fish in front of the moving trawl. At light intensities above the threshold measured in the tanks, the fish appeared to be oriented with respect to the groundrope and moving away from it. Below the visual threshold the fish appeared to be less active and less well oriented even when in close proximity to the groundrope. The authors conclude that herding as an effect of visual stimuli obviously may be an important part of the efficiency of the gear and that this effect may be increased by making the bridles and the gear more conspicuous. The towing speed was also found to be of importance for the herding, falling off at speeds about 3 kn. There is thus apparently a balance between the herding properties of the gear and the towing speed which result in a maximum efficiency. At relatively low speeds fish may also swim away from the gear laterally and escape. Blaxter and Dickson (1959) observed the swimming speeds of various fish and found that a medium sized cod and haddock could swim at a maximum speed of about 2 m/sec (4 kn). They could swim near this average maximum speed for up to 300 times their body length. In order to escape capture the fish must, however, swim at a lateral angle relative to the path of the trawl since all observations agree in showing that gadoids do not generally escape upwards over the headline.

Blaxter et al. (1964) may have overrated the general significance of the results of their tank experiments when they concluded that at low light intensities the reactions of fish to moving fishing gears will be minimal. Beamish (1967) reporting on photographic observations on the reactions of fish ahead of otter trawls found for haddock that most of the observed specimens swam within 40° of the direction of the two and over half were within a few degrees. After dark orientation to the direction of the tow increased. Cod was found in the day to swim in the direction of the tow ahead of the net. In a general review of the reaction of fish to fishing gear Mohr (1960) points out that results of midwater trawling experiments at night and in low light intensities indicate that other than visual stimuli may play an important part in the mechanisms by which fish react to this gear. Mohr also thinks that the towing speed is of great importance for the efficiency of trawls: a too high speed may set up escape reactions in fish at distances from the net where they can still easily escape while a too low speed may allow fish already within the net to swim away from it.

As regards other types of gear, Sundnes (1964) reports after having observed the behaviour of the Lofoten cod with the help of echo sounders that little or no reactions to purse seine sets could be seen. The fish layer was, however, broken where gill nets were located. There are otherwise a great number of observations from other fish than gadoids demonstrating the importance of the visibility of gill nets for their catching power cf. Mohr (1960).

Only a few observations are available on the reactions of gadoids to artificial light. Dannevig (1932) found that adult cod in an aquarium aggregated at low or intermediate light intensities and turned away from bright daylight and bright artificial light. Sundnes (1964) found that light at night resulted in tendencies of schooling and downward movement of the pelagic layer of spawning cod at Lofoten. Blaxter and Parrish (1958) tested the reaction of whiting to artificial light and found that this species would aggregate at some distance below the light source, the optimum light intensity being about 0.1 lux (this was much less than for clupeoids). During the day the whiting was observed to move to a depth where the light intensity was similar (0.17 lux) to that at which they aggregated during the experiments.

In a discussion of the effects of light on the behaviour and distribution of demersal fish Woodhead (1964, 1) lists estimates of the approximate depths of penetration of sunlight and moonlight into various seas in relation to minimum intensity for vision in fish. This depth varies greatly with turbidity and for sunlight the depth would be from 20 m in very turbid harbours and estuaries to 900 m in the clearest oceanic water. In the southern North Sea the estimate would be about 120 m i.e. deeper than the bottom and in the Barents Sea about 500 m. The threshold depths for moonlight are about half of those for sunlight. The important effects of light on gadoid fish behaviour is clearly demonstrated by the changes in the depth distribution and the schooling behaviour of these species which in general closely follow the daylight variations.

3.2 Response to mechanical stimuli

Sound waves are perceived by the inner ear (hearing) and local water displacements near the body of the fish are sensed by the lateral-line organs. The limits between these two types of perception are not fully known and defined.

3.2.1 Hearing It seems to be generally agreed that hearing is relatively poorly developed in marine fish, cf. Chapman (1964). Sound perception is restricted to frequencies below about 1000 Hz and ability to locate the direction of the sound source is probably poor, cf. Mohr (1960). Olsen (1967) measured acoustic thresholds in cod by conditioning experiments and compared the results with measurements of the noise levels generated by two research ships. It was concluded that the ship noise would be perceived by cod at distances up to at least 70 to 80 m. Another interesting possibility indicated by the results of these experiments is that at low frequencies (below 350 to 400 Hz) perception by the lateral line organs or skin receptors rather than by the ear may occur. If this is so, one consequence would be that the fish may have a far better possibility for directional hearing than has been thought up till now.

There are some observations on record of the reaction of fish to noise in the sea. Chapman (1964) says that "strange" sounds may sometimes induce "fright" responses in schooling fish. These reactions are observed at the commencement of the sound and if it continues the fish appear to get used to it and "normal" behaviour returns. Schärfe (1956) observed the noise produced by the rolling iron bobbin chain of a towed trawl as a marked disturbance on an echo sounder and he concluded that since cod and haddock were caught in appreciable quantities in these tows, these species were apparently not sensitive to this type of noise. Mohr (1960) cites an observation by Aslanova made from a diving craft to the effect that cod and haddock did not react to the noise from the ship's motor or propeller nor to hammering with metal objects inside the craft.

Norwegian hand line fishermen, on the other hand, sometimes use sharp noises to activate cod lost near the surface and which float around half dazed. The reaction of the fish to these noises is probably only a swimming response which may sometimes bring the fish within reach of the vessel.

Another observation made by the review author on this subject is that catches of cod by a diesel engined research vessel in very shallow waters (50 m and less) were frequently much less than expected from inspection of the echo records made during the hauls and in the area in general. Olsen's observations of the acoustic thresholds of cod referred to above show that the ship's noise may well have been perceived by cod at this depth and an escape reaction induced.

It is generally agreed that fish do not react to the high-frequency sounds used in echo sounders, cf. Schärfe (1951), Steinberg (1957), and Mohr (1960).

3.2.2 Lateral-line perception From their anatomy, it is clear that these sense organs record currents and small displacements of the water near the body of the fish, and aquaria experiments have indeed demonstrated that fish can in this way locate moving objects within relatively short distances, cf. Dijkgraaf (1963). These organs are probably of importance for the schooling ability of fish and they are no doubt also active in determining the reactions of fish to moving fishing gears. There is, however, a regrettable lack of more precise knowledge of the function of the lateral-line system, the type of stimuli that they perceive and their threshold values. As mentioned above, Olsen (1967) suggests that low-frequency sound waves may be perceived by the lateral-line organs. Chapman (1964) did some tank experiments to test the effect of low frequency vibrations on cod and herring, but results were on the whole negative. He still maintains, however, that this type of sensing may be important in determining the behaviour of fish to the approaching trawl and in bringing about escape once the fish are in the net.

Response to mechanical stimuli seems to be the only plausible explanation of herding and fright reactions induced by moving gear in the absence of light or at very low light intensities as reported by Bagenal (1958), Beamish (1967) and Mohr (1960). The last mentioned author also refers to some evidence that tactile and "distant tactile" perception may be of importance in reactions of fish to such passive gears as gill nets and long-lines. Gears made of softer material were in some cases shown to be more "fishable" than comparable gears of harder material.

As a conclusion one might say that studies of the response of fish to mechanical stimuli has been a neglected field. Its significance to fishing techniques is perhaps of even greater importance in fisheries for pelagic schooling fish and especially in purse seining, but it may also have considerable bearing on gear construction and fishing tactics in fisheries for gadoids.

3.3 Response to chemical stimuli

Olfaction in fishes has been shown to be of importance in perception of food odours and alarm substances and repellents, and it may also be part of a homing or orientation mechanism during migration. The last function has been demonstrated for salmon, but not yet for purely marine species. Most of our knowledge of this type of sensing in fish is derived from aquaria experiments with freshwater fish, cf. Brown (1957). As to, for instance, alarm substances, they were identified in some freshwater species as an excretion from injured fish causing an alarm reaction among its fellows in a school. This type of reaction has apparently not been described for marine species, but it may well be present in non-predatory schooling marine fish as well since it would signify a general survival advantage to the group. Various chemical substances have been shown to have a repellent effect on fish, cf. shark deterrents. Such substances could be useful tools in controlling school movements in purse seine fisheries.

Every long-line fisherman knows that the quality of his bait may greatly influence his catch. Martin and McCracken (1954) studied the relative efficacy of baits in line fisheries for hake, cod and haddock and found that the catch varied greatly between the various types of bait, from about four to about ten times in different experiments. It seemed that besides the quality of the bait, its staying power on the hooks was of importance for the fishing results.

Attempts have been made to make artificial baits that would attract fish by their smell or taste, but so far without success. This is, however, a subject that is worth further studies since line fishing could be revolutionised if the cost of the bait and the labour involved in baiting could be significantly reduced.

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SOME NEW THOUGHTS ON THE SCHOOLING OF FISHES

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Abstract

The review discusses the problem of defining a school. Spatial arrangements of fish within a school and methods of measuring school structure are discussed. Some new studies on sensory components as related to parallel orientation, communications and advantages of living in a school are put forward.

QUELQUES IDEES NOUVELLES SUR LES BANCS DE POISSONS

Résumé

L'auteur se penche sur le problème de la définition d'un banc de poissons, examinant notamment la distribution spatiale des poissons dans le banc et les méthodes permettant de mesurer la structure de celui-ci. Il étudie certains aspects nouveaux intéressant les récepteurs sensoriels dans leurs rapports avec l'orientation parallèle, les communications, et les avantages que présente la vie grégaire.

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NUEVAS IDEAS SOBRE LA AGRUPACION DE PECES

Extracto

Se reseñan los problemas que plantea el tratar de definir lo que constituye un cardumen. Se examina la distribución de los peces dentro de un cardumen y los métodos para calcular su estructura. Se mencionan estudios nuevos sobre las componentes sensoriales relacionadas con la orientación en paralelo, las comunicaciones y las ventajas de vivir en un cardumen.

1 INTRODUCTION

The fact that fishes form into schools has been an extremely important aspect in the development of many commercial fisheries. Without schooling behavior the taking of fishes such as herring in the sea would have been economically unfeasible. Because of schooling, fishes are a major source of inexpensive food, easily located and taken. Parr's pioneering paper (1927) attests to the fact that it was really those individuals concerned with commercial fishing who first began to investigate the nature of schooling behavior. His main interest, however, was not to tell where and how to harvest schooling fishes, but rather, his chief aim was to take the mysticism out of schooling and to put it on a firm biological basis. Even now, his paper continues to be thought-provoking with its numerous ideas neither affirmed nor rejected.

2 TO DEFINE A SCHOOL

Parr pointed out that schooling has been interpreted as a social instinct "in an anthropomorphic way assuming the school to be the result of deliberate activities of the single individuals seeking the protection of great numbers, thus each acting with the school as a whole as their aim". Based essentially on the visual system, schooling behavior came about through "mutual attraction and adjustment of direction, with the latter checking the approach". These he considered "as automatic responses originating from a specialized tropism". However, in clairvoyant anticipation of present problems in defining a school he pointed out that there were differences among certain fish groupings. Although the end result was the same, that is, a group formed, the forces which brought it about were based on significantly different biological factors. Parr, tackling the problem of how to classify fish groupings, essentially separated those fish that only occasionally school and those that school all the time. The first group was identified by their reaction to stimuli created by a temporary situation, the gathering and dispersing of those schools seems to be determined by immediate environmental factors. Parr's other group 'true schoolers' "are characterized by great stability through the most varied of environmental conditions". The fact of their stability suggested to Parr that the maintenance of these schools, e.g. mackerel, herring, is dominated by internal factors and in his paper he considered only the second group. Allee's work (1931) gave considerable impetus to the study of social groupings. At that time it was clearly recognized that there were two main types of groupings, one showed grouping behavior because each member was attracted to the same place, based on common response to similar physical environmental conditions e.g. light, temperature and, at the same time, each member tolerated the proximity of other members. In that type, mutual attraction between species members played an insignificant role, if at all. The second type of grouping was based on mutual attraction among species mates with a range in the intensity of attraction, some strong, some weak. In this social grouping, physical environmental conditions played a secondary role, if at all. (Allee proposed an elaborate system of classification, listing more than 50 separate categories for almost any social exigency and/or biological change during the life of the animal. The categories were unwieldy and their non-use attests to their unworkableness).

Allee's work eventually stimulated many analyses about the physiological advantages of living in communities, but until 1946, schooling, as such, was not examined, except for two papers, one by Spooner (1931) and the other by Schlaifer (1942). Each dealt with the sensory modalities employed during schooling. In 1946, Breder and Halpern presented some thoughts and experiments on aggregations in fishes and reopened the question of when is a group of fish called a school and when is it called an aggregation. They pointed out that schooling is an extreme form of the aggregating tendency. The distinguishing features of a school are that all individuals are similarly oriented, uniformly spaced and moving at a uniform pace. They recognized, however, that an accurate definition could not be easily stated because there was considerable flux in orientation, spacing and speed in many of the species studied. At one time the same group of fish showed uniformity of spacing and orientation, at another time, randomness in their orientation, although they remained as an aggregate.

Some readers may believe that the distinctions between aggregations and schools are trivial semantics. But it was a step forward in the early studies of social behavior to distinguish aggregations that occurred because all the animals came to the light source, for example, or those that occurred because they were attracted to one another. Nonetheless we were burdened with the word aggregation by which some authors meant a grouping formed because of similar responses to external physical conditions and other authors meant a grouping, without infering its casual nature. Breder and Halpern's suggestion that schooling is an extreme form of the aggregating tendency, where aggregation is based on mutual attraction was a breath of fresh air. Schooling was given a characteristic geometry.

In his excellent review, Morrow (1948) slipping away from Breder's definition, considered aggregation as "a chance grouping of individuals brought into a given locality by some external factor or factors not concerned with relationships between individuals, and schools as a closely knit cohesive group, in which there appears to be a definite centripetal influence existing between fish and fish". Atz (1953) defined schools in the terms of Breder (1946) and added that the term aggregation should be reserved for fish showing mutual social attraction, but that have no uniform orientation. Keenleyside (1955) called the school "an aggregation formed when one fish reacts to one or more fish by staying near them... The chief factor... is a definite mutual attraction between individuals". At this point, the reader can clearly see that school terminology had become a personal preference and that an operational definition of schooling was sorely needed.

Breder (1959) offered such an operational definition. He kept schooling behavior as an aggregating tendency with a distinction being made on the basis of school structure, namely spacing, parallel orientation and concomitant movement. In each condition, aggregation or schooling, the fish are brought together on the basis of mutual attraction, largely independent of environmental circumstances. In aggregation, the geometric orientation is random. In schooling, it is polarized.

Williams (1964) in a paper on the evolution of schooling embraced the attitude of Keenleyside and used the term school to refer "to any contagious distribution that owes its persistence to social (but not sexual) forces". When he referred to aggregation, he referred to groups of individuals independently seeking the same localized conditions, as did Morrow. His term school was used to designate fish groupings that are based on mutual attraction. They can show little or no polarization or a high level of polarization, in the definition of Breder. Again, the only place where there is agreement among authors is that a school is based on mutual attraction of fish.

It is unfortunate that Williams reverted back to earlier distinctions because students of schooling and especially the outstanding student, Breder, has become accustomed to using both terms, aggregation and school, to designate a biosocial phenomenon in which the groupings differ in their internal organization. Recently additional distinctions based on biological forces were suggested by Tobach and Schneirla (1968). Although they were not concerned with schooling, per se, their categories are appropriate to this discussion. Tobach and Schneirla had subdivided associations, collection of two or more individuals, into two types of aggregations, one passive, as the result of wind or waves driving animals together and the other active, "as a result of responses of individual organisms to stimulation from an external source". This latter association is generally the result of taxis involving the movement of the organisms to a place. However, the external source could be another animal and thus could be called a biotaxic reaction. "Aggregations based upon biotaxic responses may provide the setting for the reciprocal stimulation of the collected animals". Tobach and Schneirla termed the type of group bond formed in such animals as a "bio-social" type. These animals are "capable of behavioral modification within distinct limits: and their activities are determined by 'structural and physiological factors'". Schooling behavior fits into their definition of aggregations based on biotaxic responses.

At this moment, it is necessary to leave it to the reader to decide if he wishes to call a school a grouping based on mutual attraction, with rather specific geometrical qualities or if he wishes to call a school any grouping based on mutual attraction, and assume that the geometry of the grouping is an irrelevancy. My own opinion is that Breder's definitions are workable and that aggregation as well as schooling is a biosocial phenomenon. A common element of aggregation and of schooling is mutual attraction (and approach). Mutual attraction is probably based on higher neural processes which are concerned with species discrimination, involving responses to specific cues, filtering mechanisms, experimental factors etc. These processes, considered as first order are incorporated into the formation of aggregates and schools. Now this is where the distinction between aggregation and schooling can be made. Schooling incorporates a second order, based on lower neural processes, which results in the characteristic geometry of schools, their spacing, their movement and their parallel orientation. Of course, the possibility remains that some aspects of mutual attraction among schooling fishes are based on factors, such as movement, which belong to the second order.

I believe that examining these biosocial groupings as first order and second order factors will eliminate the objections that authors have to one another's definitions of schooling. For example, studies of mutual attraction in Pristella sp. by Keenleyside (1955) are on the first order, effects of environmental variables on school structure (Hunter, 1966, Cullen, Shaw and Baldwin, 1965) are on the second order.

3 THE GEOMETRY OF SCHOOLS

It is no longer truly adequate to describe fish schools in an anecdotal way, such as saying that fish in a school have spread apart or drawn closer. Although such description may have immediate value at sea, it cannot be used for comparative studies, among different species, nor can it be used for comparisons of the influence of environmental conditions on the school's behavior. In order to analyze the effects of environmental variables on school structure and behavior, of pertinent and practical value to the fishing industry, it is recognized that there is a need for precise measurements of school structure and changes in behavior. We qualitatively recognize certain features of schools such as similarity in speed among fish, parallel orientation, spacing and the strong tendency to return to the schooling state after a disruptive influence. In 1954 Breder, attempting to quantify these qualitative characteristics, proposed a set of equations describing fish-to-fish spacing and in addition he made measurements of fish-to-fish distances taken from photographs. However, his measurements did not allow for the fact that schools are three-dimensional and that small distances in the relative height of two fish above the bottom can substantially affect their distances apart. Recently there have been a number of papers in which authors tackled the problem of measuring the fish school. Each author was faced with the decision as to what kinds of measurements would be most useful, simple to carry out, and adaptable to a variety of species. Hunter's (1966) paper sums up the techniques proposed by several authors. They include: "rank estimates of the degree of aggregation (Bowen, 1931): measurements from photographs of the distance between two parallel fish in a school (Breder, 1954): density measurements based on visual approximation of the position of fish against vertical and horizontal grids (Keenleyside, 1955): calculations of swimming speeds from cinematographic data (Steven, 1959): and the perimeter of the smallest polygon which encloses a school (Williams, 1964). John (1964) developed an index of schooling based on the assignment of a rank to each possible horizontal grouping of six fish. If only two of the fish were near each other, the value 1 was used; if all fish were together, the value 10 was used; and intermediate groupings were assigned ranks between 1 and 10. Hunter, in that work, developed his own technique for the measurement of school structure, in a horizontal plane, from motion pictures. Most other authors, except Keenleyside, also studied schools as if they occupied only horizontal plane. All were aware of this discrepancy and they adjusted for the depth dimension by keeping fish in very shallow water where the animals were forced to assume a horizontally compressed shape. Keenleyside (1955) took account of the three dimensional structure by considering the density of fish in a space.

What are the most useful measures that can tell us about the spatial qualities of fish schools? Measuring the perimeter of a school tells nothing about orientation within the school, fish-to-fish distances, etc. Ranking fish gives no quantitative measures of fish-to-fish distance. Density measurements ignore orientation, although cohesion can be examined. Fish can be closely packed, but quite randomly oriented. Thus, one can get measurements of space occupied by a school without knowing the internal organization of the school. Several researchers have attempted to overcome these limitations. Cullen, Shaw and Baldwin (1965) developed two techniques, one utilizing stereophotography and the other utilizing the shadow cast by individual fish, for the study of three dimensional schools. Dambach (1963) reported a way of determining the depth of fish in water from vertical photographs which in essence is similar to the shadow method developed by Cullen, Shaw and Baldwin. The latter authors measured, from photographs of schools, the following; the distance between the head of each fish and the head of its nearest neighbor in whichever direction it may have been, the angular heading of the fish relative to each other, the compactness or dispersion of a school and its shape, that is, whether longer than broad, etc. and the volume occupied by a school. The results of their study indicated that fish are packed together equally tightly in all planes and that diagonal positions tend to be favoured in preference to those in front of, or behind the fish, or directly abeam. "It is as if there were a roughly spherical bubble around the head of each fish which is maintained in contact at some point with the bubble of another fish". The diameter of the bubble for Harengula would be 3 to 6 cm, so that much of the body and tail of the fish would project behind it. The spatial preferences corresponded to the observations and analyses of Breder (1965) in his study of fish vortices and schools. He proposed that vortices "cast off by each fish" are critical to fish spacing. Probably the most uncomfortable place for a fish to be would be directly behind the tail of another fish, since it would be constantly buffeted by the turbulence created by tailbeats.

Hunter (1966) calculated mean separation distance, mean distance to the nearest neighbor, and mean angular deviation. He then applied these measurements to schools of six fish. Hunter pointed out that separation distance to nearest neighbor are competent parameters and that "for a relative measure of changes in spacing of an entire school, separation distance is preferable, but for a comparison of samples containing different numbers of individuals...distance to nearest neighbor must be used". As an example of how these measurements can be applied and can give specific reproducible data, Hunter (1968) measured schools of jack mackerel under various light intensity conditions. He found that mean angular deviation dropped from 60° at 6×10^{-7} foot-lamberts to approximately 25° at 6×10^{-6} foot-lamberts and that mean separation distance was significantly reduced as the light increased from 6×10^{-6}, as was mean distance to the nearest neighbor.

Measurement of angular headings tell the investigator about the intensity of parallel orientation. If two fish are exactly parallel their angular divergence from one another is 0°. But at what angular headings are the fish no longer considered parallel as the term is used by students of schooling? Angular deviation cannot stand alone as a measurement since fish can be parallel and 100 ft apart. Thus, separation distances between fish on both horizontal and vertical planes also must be considered. Compactness and school shape can be derived from various measurements on internal structure. Actual dimensions of fish schools can be found in Dambach (1963), Cullen, Shaw and Baldwin (1965) and Hunter (1966 and 1968). Of interest, in terms of schooling development is the finding of Dambach that as Tilapia macrocephala grew, their fish-to-fish distances tended to enlarge - which brings up the question about fish spacing in relation to fish size and fish spacing in relation to numbers in a school. The techniques mentioned above can provide answers to such questions about schooling behavior.

One of the greatest problems faced by Cullen, Shaw and Baldwin and Hunter is the large amount of time required to take the measurements and the large amount of data that must be processed. These techniques cannot be quickly and easily carried out. Nor can they, at this time, be effectively used under field conditions. Through the use of scanning devices which indicate spatial location of individual fish and with a technology for automatic computation, schooling students will be able to examine schooling under a variety of environmental situations and to predict natural behavior at sea.

4 SENSORY COMPONENTS

Parr (1927) first suggested that the entire schooling mechanism, approach and adjustment of position, could be mediated through the visual system. The visual system is the only one shown unequivocally concerned with schooling. Without vision no schooling occurs (see reviews by Morrow, 1948; Atz, 1953; Breder, 1959; and Shaw, 1962) since attraction cannot occur.

The visual system can be examined from two viewpoints, one dealing with attraction and the other with orientation. Orientation follows attraction and therefore in studies dealing with orientation alterations of the visual system must not interfere with the factors of attraction. Keenleyside (1955) examined the attraction phenomena, as did other workers who blinded fish or modified vision in some way. He sought to determine the specific cues that gave rise to mutual attraction among conspecifics and among heterospecifics. He studied the reactions of the threespined stickleback (Gasterosteus aculeatus) and the rudd (Scardinius erythrophthalmus) to the visual presence of species mates and found that any single fish, separated by glass from a school, tried to approach the school. Blinded fish did not show this behavior. In other tests fish were given choices of different sizes of conspecific mates, and a variety of numbers in groups. The results were not absolutely clear but the predilections of the test fish indicated a preference for fish larger than itself and for groups composed of large numbers over small numbers when there was a wide numerical difference e.g. 12-1. Other tests showed variations in approach to heterospecifics dependent on the species being tested. After his series of experiments he concluded that, despite the tendency to approach, a single fish did not remain indefinitely near an aggregation separated from it by a glass wall. Some features made certain groups more attractive, e.g. larger numbers, size, but visual stimuli alone were inadequate to maintain the attraction. In another work on visual stimuli and attraction, Hemmings (1966a) studied the reactions of Rutilus, Mugil and Chromis to the presence of another caged fish or a mirror. Rutilus and Mugil preferred the half of the tank containing either the caged fish or the mirror whereas Chromis showed only a preference for the caged fish. Hemmings pointed out that under field conditions, Chromis responded to the mirror. The results of the control studies showed sufficient inconsistency that the author had difficulties in interpreting the significance of the experimental results. Hemmings, without stating it, realized that presenting fish with a single stimulus presented conditions of extreme artificiality. These experiments did, however, verify the primacy of the visual system for the mutual attraction that occurs in schooling fishes. The specific features that give rise to attraction are still unknown. The tendency to school is of such strength that a fish devoid of its species mates will approach almost any moving object (within a certain size range); the greater the movement, such as Keenleyside's 12 fish, the stronger is the response. But, as noted earlier, visual attraction alone did not sustain a grouping. If parallel orientation was possible fish tended to remain near one another and to swim, side by side, even if they had only visual contact (Shaw, unpublished). The orientation, however, was somewhat erratic. When fish were separated by barriers which, because of the nature of the barrier, did not permit parallel orientation, the initial attraction was not maintained. In all probability additional cues, derived from orientation, come into play with a "give and take" occurring between and among fish. Whether or not the stimuli required to maintain parallel orientation are purely visual or are of another sensory system, or several combined has not yet been elucidated. These stimuli must continue when fish are changing velocities and positions and must operate whether the fish are at the head, middle, rear, side, anywhere in the school. To see if the optomotor reflex could be employed in the parallel orientation and forward movement in the school, species of carangids were tested in an optomotor apparatus. See Shaw and Tucker (1965) for technical details about such an apparatus. They found a direct relationship between number of rotations described by the fish and drum rotations. As number of drum rotations increased so did those of the fish, and the fish was obviously orienting to the moving field of stripes. In their discussion they pointed out that in an optomotor response (1) the fish moves in the same direction as the moving field and parallel to it, (2) the fish changes its speed as the speed of the moving field changes (3) the fish alters its position relative to the field, that is it is not always opposite the same area of the stimulus. The similarity between this behavior and certain features of schooling is striking - (1) fish move in the same direction (2) a fish changes speed as the fish surrounding it change speed (3) a fish changes its position relative to other fish, but nonetheless remains parallel to the school. One point not mentioned in the paper but observed by this author in other tests with Atherina was the quickness with which the fish responded to a sudden increase or decrease in speed. If the drum, perhaps rotating at 4 r.p.m., was suddenly increased to 12 r.p.m. the fish response was almost instantaneous. It is unfortunate that no latencies were taken but it appears that they might have been under one-half second.

Other fish show the optomotor reaction such as Mugil (Horstman, 1959 and Shaw, 1965) and many other species mentioned by Harder (1963). In our laboratory, we tested Tilapia sp., Spheroides sp., Aqueidens sp., Ammodytes sp. (it often collapsed on the bottom of the aquarium as if dead). In these tests many non-schooling species, in our definition, did show the response of moving in synchrony with the moving field of stripes. In Spheroides sp. whose adults tend to live a solitary existence, juveniles showed a classic response. It must be noted that these fish tend to aggregate as juveniles. Tilapia macrochephala showed a somewhat erratic responsiveness, with many juveniles displaying movements up and down the cylinder and not moving with the stripes. Good and bad responses were highly individualistic. A few fish gave consistently good responses and others gave consistently uneven responses. However, when these fish were treated with frenquel, a tranquilizer, the erratic movements (sometimes called escape reactions) disappeared and the optomotor response became smooth and classic. This points to the possibility that the variability mentioned by Shaw and Sachs (1967) was caused by fear or stress induced by the apparatus; with the elimination of the fear or stress the response became consistently smooth in all fish. In the optomotor apparatus important features of schooling were reproduced. It was suggested by Shaw and Tucker (1965) that fish in a school may be providing, for other fish, a series of successive contrasts, greatly enhanced when fish are moving. Since Baylor and Shaw (1962) found that the eye of many schooling species was far-sighted in the lateral field, it may be well suited to responding to small movements with concomitant enhanced contrast.

The results of some of the studies which showed that non-schooling as well as schooling fishes showed an optomotor response suggests again that schooling is a double-order system. Parallel orientation is more of a reflex system, mutual attraction is found in higher levels of nervous activity. Mutual attraction and approach are essential ingredients to fish groupings, and parallel orientation may be the result of the fish's taking a visual fix on a moving environment.

I have not mentioned very much about the lateral line system. It has become a favorite subject in the study of schooling because of recent work by Harris and VanBerjeick (1962) where they showed that neuromasts within the head canals of the lateral line are sensitive to "near-field water displacements". This sensitivity could be employed by fish in their parallel orientation and spacing and be most effective in the fine adjustments that the fish make to one another, spatially. Cahn, Shaw and Atz (1968) found that lateral line neuromasts are innervated at the time parallel orientation begins in Menidia. This also points to the involvement of the lateral line in fish orientation and spacing. Unfortunately the hydrodynamics of the school are known only vaguely and we are not certain of the water patterns surrounding each fish. Breder (1965) discussed hydrodynamics of schooling at length, in terms of vortices produced by swimming fish. Understanding the boundary layers surrounding each fish is imperative to our understanding of the lateral line and its function in schooling. The interplay of boundary layers and vortices needs clarification.

In other experiments on sensory components and their role in schooling, Hemmings (1966) studying olfaction as an attraction phenomenon compared response of Rutilus to odors from live, healthy conspecifics and the skin derivatives of killed conspecifics. "Positive reaction to the odour from undamaged fish was rather less strong than the "Schreckreaktion" or negative response to the odour of damaged fish. This difference occurred because all the fish when tested showed a strong response to the Schreckstoff, but some fish showed very little response to the attractant odour". The experiments do not really define the role of olfaction in schooling although Hemmings suggests that the fish remain by night partly through an olfactory mechanism.

Stevens (1959) examined the problem of olfaction as a stimulus for mutual attraction and found that many extracts provoke "feeding behavior". Hemmings did not consider the possibility that attraction-approach occurred on that basis. The study of olfaction even under the most rigidly controlled conditions is difficult, presenting numerous technological problems and often unclear results (Kleerekoper, 1967). In the above experiments, the role of olfaction, as an attraction-approach mechanism was not delineated.

5 COMMUNICATION

A most striking feature of fish schools is their apparent synchrony of action. How are changes in direction, speed, positional orientation in one fish communicated to other fish? By what means do the fish maintain the integrity of the school? The visual signal was offered as a means of school maintenance earlier in the discussion of the optomotor response. Acoustic signaling has been explored by Moulton (1960) but Breder (1967) does not believe that sounds are employed by schooling fish for communication. In fact, he pointed out that schools have a tendency to be relatively quiet, except for swimming and feeding noises. It seems strange that at this late stage of studying schools we have not carried out the simplest observation, one which can give us considerable information about speed of responses of fish in schools. Such information could indicate what communication channels to look for. The most direct approach to the analysis of speed of response is through the use of motion pictures. I have examined frame by frame a series of motion pictures taken of a school of Harengula sp. in the waters of Bermuda. During the course of photographing the school, the entire school changed direction, perpendicular to its original course. It was noted that the change in direction occurred in pockets, that is, within the school, three or four fish turned 90°, as a group, and there were three such groups formed before the entire school turned. Interestingly, the groups or pockets were inside of the school, not at the edge and they were not contiguous, but disparate. However, once the pockets had turned the remainder of the school turned almost simultaneously. The entire action occurred within one-half second.

These observations, unfortunately only on one school, under one special set of conditions, illustrated that responsiveness of fish-to-fish may be more complex than we thought. Many students of schooling have noted that in schools of 50 or more fish several fish can break away, alter direction and not in the least affect the directionality of the school. These fish will often return to the school within seconds of their diversion. Yet under other conditions, a small group of fish, changing their direction will influence the behavior of the rest of the school, which, in turn, changes direction.

At this time, we must accept the fact that the degree to which any fish or group of fish influence the behavior of the entire school is unknown. We do not, indeed, even know whether a change in orientation of one or several fish causes a direct change in the others. The possibility exists that several fish are reacting independently to an environmental stimulus sooner than other fish and as a result they change orientation sooner. Reorientation of the entire school could be dependent on each fish within the school responding individually to the external stimulus. But this is unlikely and inefficient for the school. Each fish is a discrete unit and all the fish around it are external stimuli. It is distinctly advantageous in school living to react to neighboring fish without perceiving the original source of stimulation, such as for example, a predator swooping down on a school.

In all likelihood this is what occurs under some conditions. A small unit of fish (within a large school) react to an outside stimulus and the unit changes direction or reorients. The main body becomes alerted to the reorientation and they react to it initially, not to the outside stimulus. The outside stimulus, now perceived by the main body, functions in reinforcing the reorientation.

One feature of schooling that is often mentioned and accepted as part of schooling behavior are the small shifts in orientation and small adjustments of speed. This can be seen in individual fish and in small groups within a large school. I should like to suggest that these adjustments provide the school with a scanning system which makes the school more alert to environmental changes. Through information, external or internal, received by any one of these units, the internal structure of the school can be modified. Because schooling fish respond to adjustments in neighboring fish, scanning by discrete units may be an adaptive feature of life in a school.

6 PHYSIOLOGY OF SCHOOLS

Thines and Vandenbussche (1966) used the alarm reaction to produce schooling among Rasbora heteromorpha under conditions of night and day. They were examining the premise that schooling tended to disperse at night because "visual information progressively diminishes". They suggested, instead, as a possibility "that dispersion may also be partly due to a decline in the responsiveness to external stimuli". In their tests they used a skin-derivative which, when introduced into a tank of fish, resulted in increased cohesion or a more intense coming together of the fish. They found that school cohesiveness was dependent on illumination only to a certain extent. With bright light, at night, school cohesiveness was not as great as it was during the day with comparable light intensity. Unfortunately the experiments have a number of loopholes. For example, turning on a light for 25 min at midnight may be an inadequate period of time for the reappearance of schooling behavior. Since the skin derivative was freshly prepared the authors could not be sure that the substance taken from fish during the day and night were equivalent in potency. And perhaps most important of all, although schools were produced under the test conditions the factors of production may have no relevance to the factors that produce schooling behavior as we have been examining it.

Nevertheless, these experiments do open an extremely interesting avenue of research, namely, that fish-to-fish distances and, in general, the entire behavior of the school may have a basic circadian rhythm, reinforced by changes in the external environment. We have, in the past, assumed that organization was entirely dependent on the physical environment, as for example, schools dispersing under certain conditions of light. Now, more considerations must be given to the physiological condition of the fish.

The entire area of the physiological condition of fish and their schooling behavior is one that has not been extensively examined except for Hunter (1966) who demonstrated that when fish were deprived of food their schools tended to be less cohesive and after feeding they tended to become more cohesive.

The internal state of each fish can influence the internal structure of the school. An approach to that aspect was made by McFarland and Moss (1967) who were concerned with the "whys" of change in school shape. Many factors exist that could modify the direction and movements of a school, factors, such as temperature, salinity, water currents, bottom contours, etc., in addition to that vaguely defined factor "the tendency to school". McFarland and Moss, in their original study, proposed that respiratory gases may effect certain changes in school structure in Mugil cephalus. They suggested that "reduction of dissolved oxygen and increase of carbon dioxide from school metabolism may be sensed by individual fish. This detection of altered environmental gas concentration could induce modified behaviors such as change in direction, spacing and swimming velocity". They measured oxygen and pH (for CO_2 determination) and found a reduction in environmental oxygen, correlating with school size, a "large school" having the greatest oxygen reduction. They postulate that schools may break up when there is "severe metabolic reduction of environmental oxygen". The suggestions made by these authors are stimulating and it is hoped they will continue. Unfortunately one does not know what they mean by small, medium and large schools and one does not have any idea of the effect of the observers on the school. If the investigator placed an electrode into a densely packed school, would the school not disperse out of fright? Perhaps the oxygen depletion was a result of increased breathing as a result of fright. This author believes that the investigative methods were an important influence on the data obtained. The results would be convincing if greater controls had been taken not to influence fish behavior by human behavior. That the metabolic state of each fish affects schooling is undoubtedly true and we must now carefully examine the correlates of physiology and behavior.

7 EVOLUTION AND ADAPTIVE ADVANTAGES OF SCHOOLING

We cannot deduce the origin of schooling behavior from the fossil record. True, many fossil fishes are found in great clumps but the dangers are apparent of inferring group behavior from these associations. Nonetheless, the evolution of schooling challenges the biologist for it has appeared in a number of families ranging from the primitive herrings to the advanced tunas. And if the definition of schooling is extended as it is by some authors to cover non-polarized groupings then even more families are included. In addition, many fish school in the juvenile stage although they do not show this behavior as adults, e.g. barracuda. Schooling must be assumed to be adaptive by its quasi-unversatility among fish species. The adaptive value of schooling has been discussed by a number of authors, most recently in the work of Breder (1967) who reviewed earlier studies. Many offerings for adaptation have been made ranging from reproductive facilitation (Parr, 1927) to energy conservation (Shaw, 1962). Perhaps the earliest were studies of "group effect". These were not directed at schooling, per se, but at the advantages of group living. The goldfish was the classic test fish and it was found that poisons were not as detrimental to fish living in groups as they were to fish living alone. Oxygen consumption per fish was lower among group living forms than in an individual fish of the same species. These tests failed to take into account the stressful effect of removing a normally social fish from its group. Increased oxygen consumption may have nothing to do with the ephemeral "group life", but may be concerned with increased activity because of distress. In that connection, Alekseeva (1963) found a "group effect" when individual fish were visually isolated from the group, but could not obtain a "group effect" oxygen consumption rate when an individual had only visual access to species mates. "Group effect" had not been critically tested and cannot be assumed an adaptive advantage of schooling at this time. Another suggestion, also untried, is that fish living in a school can utilize energy produced by the swimming motions of surrounding fish (Shaw, 1962 and Breder, 1965). In an extended analysis Breder (1965) stated that energy as a vortex created by a swimming fish represents "the energy that the fish had expended to propel itself". Neighboring fish could utilize a vortex and coast on it thereby reducing their constant swimming effort. On occasionsan individual fish could take advantage of a "free ride"; this same fish may have to exert greater swimming effort at other times to the advantage of a neighbor.

Brock and Riffenburgh (1960) considered that schooling is a mechanism which assures the survival of the total school even when a number of school members are lost to predators. They showed by mathematical formulation that the "frequency of detection of prey by predator is an inverse function of the number of schooled or grouped prey. The quantity of fish that a predator can consume on any single encounter with a school of prey has some average limit, and once school size exceeds this quantity, further increases in school size reduce the frequency of predator-prey encounters without necessarily changing the quantity of prey consumed on the occasion of each encounter, which in turn may reduce the rate of consumption of a prey species by a predator".

Their mathematical formations, highly plausible, are not sufficiently flexible to suit the behavior observed between predator and prey schools. For example, Clarke, Flechsig and Grigg (1967) making observations from Sealab II, found that jack mackerel reacted differently to different predators. When attacked by sealions and bonitos, a common predator, they dashed off as a unit. When the jack mackerels were attacked by scorpion fish or rockfish, not common predators, only the individual attacked reacted. The authors noted that the bonito and sealion attacked from above, the others from below. I have noted that mackerel schooled below the silversides, occasionally swam up, selected an individual, and consumed it. The school remained unruffled. Predator-prey relationships and their effects on populations appear to be highly individualistic. Each predator type has its own set of interactions with each prey type, all amodified by the general environmental conditions and by numbers.

Breder (1967) evaluated the survival value of fish schools in relations to predation, water visibility, size of groupings, quietness of schools, and finally points out the "whole matter of schooling and aggregating is looked upon as a mechanism of behavioral homeostasis and as such is subject to the influence of selective pressures". Williams (1964) carried out experiments where he placed fish into a visually homogenous environment. He indicated that fish would form groups when their own visual reference point was other animals. In his interesting discussion on survival values of schooling, he summarized some of the postulates such as "schooling serves to condition the median", "relates to reproduction" and "affords protection against predators". He then proceeds to demolish each postulate which Shaw (1962) and others have done. He then proposed that "a school is not an adaptive mechanism itself, but rather an incidental consequence of adaptive individual behavior". In essence, each fish sought to associate with other fish, "schooling is a form of cover seeking". Then Williams went on to state that schooling is conspicuous in pelagic habits - not detectable in weedy areas, and intermediate in intermediate habitats. Unfortunately his argument does not withstand the acid test of underwater observations. There are schooling species in weedy and rocky areas as well as in open water areas. In fact, the atherinids, very much inshore schooling forms, are found around long rocky jetties, over weedy bottoms and great clusters can be seen in holes in the rocks. *Fundulus heteroclitus*, which fits Williams definition of a school, is distributed among grasses. There is also no such thing as visually homogeneous environment, the moment that there is more than one fish in the environment. Nevertheless, Williams has provided some stimulating ideas about schooling evolution, but his theories do not adequately satisfy the facts of schools.

My belief is that we are making a serious error in attempting to find a single adaptive feature for schooling. There is survival value in schools, not as a result of single features but rather as a compounding of many adaptive features, each one small and not able to stand alone. The group effect, the confusion effect, (Welty, 1934) reproductive facilitation, social facilitation, large numbers, mimicry in appearing as a large animal, energy conservation, etc., all these in conjunction can make schooling behavior highly adaptive.

In summary, I have tried to present some of the newer studies on schooling behavior. Breder (1959) and Shaw (1962) survey the earlier state of knowledge of schooling behavior and I refer readers, who wish to fill in the details, to those papers.

In this brief review, I have covered the problem of what is a school, by definition; the spatial arrangements of fish within a school; methods of measuring school structure; some new studies on sensory components as related to parallel orientation; communications, and new thoughts on the advantages of living life in a school.

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A REVIEW OF SOME EXPERIMENTAL STUDIES OF FISH REACTIONS TO STATIONARY AND MOVING OBJECTS OF RELEVANCE TO FISH CAPTURE PROCESSES

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Abstract

This contribution reviews the results of work done in tanks and in the field on the behavioural responses of fish to stationary and moving objects, of relevance to fish capture processes. Reference is made particularly to the differences in the responses of the fish to such objects and fishing gears in daylight and darkness and the relative importance of visual and non-visual stimuli is discussed.

EXAMEN D'ETUDES EXPERIMENTALES SUR LES REACTIONS DU POISSON DEVANT DES OBJETS FIXES OU MOBILES, EN RAPPORT AVEC LES PROCEDES DE CAPTURE

Résumé

La communication passe en revue les résultats de travaux effectués dans des viviers ainsi que sur les lieux touchant les réactions du poisson devant des objets fixes et des objets mobiles, en rapport avec les divers procédés de capture. L'auteur s'attache particulièrement aux différences de réponse devant ces objets et devant des engins de pêche selon que l'animal se trouve à la lumière du jour ou dans l'obscurité, et étudie l'importance relative des stimuli visuels et non visuels.

R/12

RESEÑA DE ESTUDIOS EXPERIMENTALES DE LAS REACCIONES DE LOS PECES ANTE OBJETOS MOVILES E INMOVILES DE IMPORTANCIA EN LOS METODOS DE CAPTURA

Extracto

Reseña el autor los resultados de investigaciones realizadas en estanques y en el mar respecto a las reacciones de peces ante objetos móviles e inmóviles, que influyen en los métodos de pesca. So refiere en particular a las diferentes reacciones de los peces ante tales objetos y artes de pesca durante el día y la noche y comenta la importancia relativa de los estímulos visuales y no visuales.

1 INTRODUCTION

It is now fully recognized that the process of fish capture by a fishing gear involves a complex of interactions between, on the one hand, the physical properties of the gear itself and, on the other the behavioural properties of the fish subject to capture. Hitherto, approaches to the problem of increasing the efficiency[1] of fish capture, have been mostly confined to consideration of the first of these factors, with little reference to or in ignorance of the second. Although this type of approach has resulted in some notable successes, as, for example, the introduction in trawling of sweeps and bridles between the otter boards and the wing-ends of the net, it has also resulted in some disappointing and costly failures due to the lack of appreciation and understanding of the behavioural properties of the fish in relation to the changed complex of physical stimuli generated by the new or modified gear. Considerations of both sets of factors together is therefore necessary in the approach to this problem, involving close collaboration between gear technologists and fish behaviourists.

The main reason for the lack of attention in the past to the fish behavioural factors in relation to marine fish capture was the difficulty involved in making detailed observations of fish in the vicinity of fishing gears. Comparative fishing experiments, in which the "old" and "new" gears (e.g. in design, rigging and/or method of operation) are fished together under controlled conditions have yielded (and will continue to do so) some valuable results on their relative catching efficiencies, which in many instances have been directly applicable in commercial fishing operations, but they provide no direct information on the capture processes involved and on the specific factor(s) causing the efficiency change. Furthermore, such experiments are both costly and time consuming, especially if, as is desirable, each one is carried out over as wide a range as possible of the conditions experienced in practical fishing operations. Therefore, in addition to this type of empirical approach, which, I wish to emphasise, is often of great value in providing the initial pointers to profitable developments in gear design and operation and in finally establishing the merits of a particular development under commercial fishing conditions, it is of major importance that more direct, observational and experimental methods of studying the fishing gear itself, the stimuli generated by it and the reactions of fish to them are applied to this problem.

In recent years attention has been directed towards the development and application of such techniques. The following main approaches have been and are being followed:-

(a) Observations on the behaviour of fish in aquaria, and in particular their responses to stimuli generated by stationary and moving "objects" (including model nets and parts of nets). The techniques used include direct visual observation; still and cine photography, television and sonar.

(b) Direct visual observations and filming by divers in shallow water at sea. The application of this method has been mostly restricted to observations of the behaviour of fish in the vicinity of full scale or model fishing gears in depths of not more than 30-40 metres in relatively clear water localities and to daylight conditions. The use of manned, underwater vehciles for direct observation and filming in deeper water is now developing rapidly.

(c) Indirect observations of fish behaviour in relation to gear in deeper water at sea, either photographically by preset or remotely controlled cine or still cameras, or by the use of sonar techniques.

This contribution summarises the results of some of the work done using these techniques, with special reference to the elucidation of the behavioural responses and patterns of behaviour of fish to the types of stimuli generated by fishing gear (or parts of fishing gear), which have an important bearing on the processes involved in capture).

1/ As used here, "efficiency of fish capture" is defined in terms of "catch-per-unit-time".

2 STATIONARY OR PASSIVE GEARS

Capture of fish by gillnets, whether anchored or floating (as, for example, in the European herring driftnet) is dependent on the activity of the fish bringing them into direct physical contact with the gear and then being held by it either by becoming "gilled" by the meshes or entangled in the netting. Clearly, therefore, the efficiency of this method of fishing is dependent on the gear generating a minimum of stimuli which provoke "avoidance" responses by the fish at a sufficient distance from it to prevent contact being made with it. Of the possible types of stimuli which might be involved, the visual ones are the most obvious and most of the experimental work conducted so far has been concerned with assessing their importance.

From observations on herring (Clupea harengus L.) in aquarium tanks, Ver heijen (1953) pointed to the importance of visual stimuli in determining their avoidance of obstacles. This was confirmed by a more extensive series of observations by Scottish workers (Blaxter and Parrish, 1959; Blaxter, Parrish and Dickson, (1964) on the reactions of small groups of herring in tanks to various types of stationary netting obstacles at different light intensities between daylight (from 10^4 to 10^5 lux) and darkness (<0.001 lux). Frames of netting made from different materials, twine thicknesses, distances between strands, mesh sizes[1] and colours were placed across the centre of the tank, and observations were then made of their movements and especially their reactions as they approached the netting, their reaction distance and the numbers making contact with or passing through it. These observations showed that in daylight the extent of avoidance of the netting obstacle varied directly with its conspicuousness. Thus, the reaction distance was greatest and the number of fish making contact with or passing through the netting was least with the thickest twine, smallest mesh size and "brightest" colour. With the least conspicuous sample of netting, made from monofilament nylon (0.2 mm diameter), avoidance reactions were relatively very small, as was also the case when a sheet of transparent plastic was used. The effectiveness of each obstacle as a barrier decreased with decrease in light intensity and at intensities less than about 0.01 lux even the obstacles which had elicited the most pronounced avoidance responses in daylight ceased to be effective, the frequency with which the herring touched or passed through them being little less than the frequency with which they crossed the same part of the tank when no netting obstacle was present.

The same general result was also obtained with a curtain of air bubbles across the tank; in daylight (when it was conspicuous), it acted as an efficient barrier to the passage of the herring along the tank, but in darkness it ceased to be so, despite its production of stimuli other than visual ones (e.g. noise and turbulence).

Mohr (1960, 1961) conducted similar tank experiments with herring and also found a direct relation between avoidance and the conspicuousness of the netting obstacles. As in the Scottish experiments, he found that netting made from monofilament twine (perlon), with a twine diameter of 0.2 mm, elicited no avoidance reactions due, presumably, to the fish not being able to perceive it. He also found that, with netting obstacles made from thicker twine, the extent of the avoidance varied inversely with the number of fish involved, the greater the number of fish (shoal size), the greater the frequency of contact with the netting. This he attributed to the influence of "shoal pressure", which may modify the fishes' reactions to external stimuli. Similar observations were made by Aslanova (1958) on anchovy.

The results of these experiments on herring are also in general accord with those from Japanese tank experiments on a number of species belonging to widely different genera (e.g. Cyprinus, Salmo, Trachurus, Atherion, Carassius, Archeilognathus) in showing the importance of vision in determining their behaviour in relation to netting and other obstacles. For example, Kusaka (1957, 1958), Hiyama, Kusaka and Kondo (1957) and Kanda, Koike and Ogura (1958) investigated specifically the effect of the colour of obstacles on the reactivity of the fish. In his experiments, Kusaka used moving instead of stationary frames of netting of different colours and his experimental technique was to drive goldfish along a tank, either from both ends towards the middle ('centralising' method) or from one end to the other ('driving to one side' method), and he assessed the effect of colour on the avoidance responses of the goldfish by counting the numbers passing through the netting. He found that red netting was the most efficient barrier, blue, green and yellow were intermediate (in that order) and transparent netting the least. A similar order of colour effect was obtained by Kanda, et al., using a different experimental method. They found that under daylight conditions the colour (i.e. the wave-length) and not its brightness was the main stimulus, whereas under twilight conditions brightness was the most important factor. Hiyama et al's experiments, on the other hand, which were conducted in brightly coloured tanks, gave different results for the avoidance of coloured tin or plastic sheets placed in the tank. Mohr (1960), in a general review of these results, suggests that this may be due to the influence of other behavioural factors associated with the brightly coloured tank.

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[1] To avoid the fish becoming "gilled" in the netting, the meshes were not knotted.

The results of the tank experiments reported above on a wide variety of species all point to visual stimuli as being of major importance in determining the avoidance responses of fish to stationary netting obstacles and hence in governing the "efficiency" of such stationary, passive fishing gears as gillnets and net traps. Clearly, therefore, it is necessary to elucidate the factors governing the visibility of such gears in the open sea where conditions are both variable and markedly different from those encountered in small aquarium tanks. Investigations of these factors have been made by Hemmings and Lythgoe (1966) and Hemmings (1966). They studied, by direct underwater observation, in daylight and darkness, the visibility to the human eye[1] of coloured synthetic fibre nets and other targets in the contrasting, shallow water conditions of the Mediterranean (Malta) and Scottish coastal waters (Moray Firth). Their observations showed that the relative visibilities of the different coloured nets and targets varied according to the water conditions and they found that the brightness contrast between the net or target and its background, rather than the colour as such, was of major significance in determing its visibility. They emphasized the importance of information on background colour and brightness in assessing the best colour for fishing nets to achieve either minimum (as for gillnets) or maximum (as, for example, for leaders of stake nets) conspicuousness. They also point out that, owing to the unequal distribution of brightness of light in the sea, perfect camouflage of a uniformly coloured net cannot be achieved, but clearly it can be approached by the correct choice of colour for the particular background conditions encountered.

The results of the tank and observational work summarized above are, in general, supported by fishing experiments with coloured gillnets in the field. Von Brandt (1953, 1954) showed that the catching capacities of semi-transparent monofilament perlon gillnets for trout in German lakes and herring in the Baltic were significantly greater than were those of coloured cotton nets. Schwartz (1958, 1959) obtained similar results for cod. In driftnet fishing for herring in the North Sea at night, however, a number of worker have failed to detect any significance between the catching capacities of nets of different colours, although fishing experiments by the

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[1] At present few data exist on the spectral sensitivity of marine fishes for photopic vision, but Lythgoe (1966) shows that the visual pigments extracted from fish eyes which, it is thought, are responsible for scotopic vision, have spectral absorption characteristics similar to those of man. Blaxter and Holliday (1963) report spectral sensitivity data for herring with a maximum in the blue-green, and they also report results by Borisov and Portasov for "anchovy", showing a maximum at 500-560 mμ.

Marine Laboratory, Aberdeen, in the northern North Sea and off the west coast of Scotland with white, green and brown nylon nets showed consistently lower catches with the white than with the green or brown ones (unpublished data). Russian observations (reported by Mohr, 1960) have shown that in driftnet fishing for herring near the surface in the Norwegian and Barents Seas in daylight, catches varied significantly with net colour; under the clear water conditions in the open sea, blue nets caught significantly more than the normal brown ones, but there was no significant net colour effect in turbid water or at night. Similar results were obtained by Aslanova (1958) in sardine fishing experiments in the Black Sea.

In summary, therefore, the results of observations and experimental work on the behaviour of fish to stationary nets and other objects demonstrate the major role of visual stimuli as factors governing the responses to them of a wide range of commercially important fish species. They indicate that these stimuli are of importance in determining the capture efficiencies of such passive fishing gears as gillnets and net traps, although, as yet there are few observational and experimental data on their role in the capture process by the latter gears. In particular, they point to the importance of brightness contrast between the gear and its background as the principal governing factor, and hence emphasise the need for further work on this factor.

This does not mean, of course, that visual stimuli are the only ones which can influence the behaviour of fish in the vicinity of these gears and hence affect their fishing capacities. As indicated by Mohr (1960), tactile stimuli, disturbance stimuli generated by the passage of water through the nets or by the presence of other fish already caught by the net, giving rise to a gear "saturation" effect (Kennedy, 1951), sound and chemical stimuli may elicit fish responses resulting in gear avoidance (or possibly attraction to the gear). Also, the responses to visual stimuli may be affected by physiological (as indicated, for example, by Aslanova's (1961) observations on the reactions to nets of Leukaspius delineatus in different feeding states), ecological (e.g. the general conditions of the environment-temperature, currents, background noise, etc.) and social (number and density of fish concentrations) factors. However, the evidence available at present suggests that visual stimuli are of primary importance under the normal operational conditions for such gears, so that with a proper understanding of the behavioural responses to them increases in capture efficiency can be achieved.

3 MOVING GEARS

Until recently, virtually nothing was known of the behaviour of fish in the vicinity of trawls and other, similar types of moving fishing gear whilst fishing. However, the recent development of new techniques of underwater observation, as well as a focus of attention on observational work in tanks, has resulted in a large increase in research on this topic.

(a) Observations in tanks

A detailed study in large tanks has been made by Scottish workers of the reactions of herring (Clupea harengus L.), haddock (Melanogrammus aeglefinus L.), cod (Gadus morhua L.), whiting (Merlangius merlangus L.) and flatfish species (principally plaice, Pleuronectes platessa) to various types of moving objects (including various types of groundropes, with and without attachments (chains, lights, floats, etc.), panels of netting of white nylon twine (4 mm diameter) of different mesh sizes and an air bubble curtain) in both daylight and darkness (Blaxter, Parrish and Meadows, 1960; Blaxter, Parrish and Dickson, 1964; Blaxter and Parrish, 1966). Their observations showed that, under visual conditions in daylight, the pattern of responses was essentially the same for all of the species studied; they reacted by turning away from and swimming in front of, and at about the same speed as the advancing object. The average reaction distance was up to 3 m (but mostly about 1 m) from the approaching object, depending on its conspicuousness and vertical extent. The warps pulling the object herded the fish inwards, while the object itself herded them forward. There was no evidence of panic responses to the approaching object, the fish becoming orientated and swimming in front, and along the line of advance of the object in a seemingly orderly manner (until the end walls of the tank were approached). The herding efficiency of the object was directly related to its conspicuousness (to the human eye). No differences in the pattern of behaviour, the reaction distances and the herding efficiency of the object were detected when sources of noise (e.g. chains attached to a groundrope, low frequency sounds from the exhaust pipe of an electricity generator) were added to the object. At low light intensities (i.e. less than about 0.5 lux), on the other hand, the herding efficiencies of the different devices decreased markedly; the "threshold" light-intensity at which the herding efficiency of an object fell to 50 percent of its value in daylight was lowest for the most conspicuous ones, and no significant difference could be detected between this "threshold" for an object when used with and without a source of additional noise. A noisy air bubble curtain, which in daylight was an efficient herding device (provided it was moved slowly enough to maintain an approximately vertical curtain of bubbles), had a very low herding efficiency at light intensities below about 0.1 lux. Other experiments were made with white and transparent model trawl-doors, moved through the tank at different speeds in both daylight and darkness. The results were essentially of the same type as with the other objects; there was a higher degree of orientation to the white door than to the transparent one in daylight, and a reduction in numbers of fish reacting to the white door in darkness.

On the basis of these observations and photographic observations on trawls at sea, Blaxter et al. (1964) concluded that the reactions observed in daylight were in response to visual stimuli and postulated that they are mainly responsible for the herding of fish by the warps and bridles of trawls into the path of the net.

A similar pattern of behaviour of young coalfish in the path of towed model trawls in tanks is reported by Radakov and Nikolaev (1957). Kusaka's experiments with moving frames of netting in tanks, reported in an earlier section, showed the same general type of behaviour for goldfish.

(b) Observations and experiments at sea

The use of aqualung diving techniques for making visual and photographic observations of the behaviour of fish in the vicinity of fishing gears and other moving objects has grown rapidly in recent years. The potentialities of this technique for this purpose were first demonstrated by the British films "Trawls in action" and "Fish and the seine-net", the latter providing useful information on the pattern of behaviour of flatfish species - mostly plaice (Pleuronectes platessa) in the vicinity of the mouth of the Danish seine whilst fishing. This technique has been applied extensively in recent years by the Marine Laboratory, Aberdeen, to study the reactions of both flatfish (plaice and flounder) and roundfish (haddock, gurnard and whiting) species to the Danish seine throughout the duration of a haul in shallow water in daylight. In addition to observations on the behaviour of the fish in the vicinity of the mouth of the net, their reactions to the ropes, to the net without its funnel or bag and to the groundrope alone have also been studied.

The principal results of these investigations reported by Parrish et al. (1964) and Hemmings (1967, this meeting) were as follows:-

(i) For all of the species observed, the pattern of behaviour in the vicinity of the mouth of the net was essentially the same, the fish being orientated away from and swimming in front of and at about the same speed as the net. Fish were caught when they stopped swimming (or swam more slowly) and were overtaken by the net. Some fish (especially flatfish) escaped capture in this way, the groundrope passing over them.

(ii) The reactions of flatfish to the ropes on either side of the net were essentially the same; they swam inwards roughly at right angles to it into the path of the advancing net. Those encountering the wing ends of the net reacted in a similar way, thereby resulting in an accumulation of fish in the centre of the net mouth. The reactions of roundfish to the ropes were not observed during these experiments, and unlike the flatfish, they first appeared in the vicinity of the net mouth in relatively large numbers in the later stages of the haul, suggesting that they had been driven into the path of the net, in response to the ropes, at a distance.

(iii) As with the observations in tanks, reported above, the behaviour of the fish was seemingly orderly; no fish were seen to move out of and away from the bight of the net mouth once they were in it and no panic reactions were observed (except by mackerel, which were observed in small numbers). As a consequence of this pattern of behaviour, so long as the speed of movement of the net was less than the sustained swimming speed of the fish (which is the case during the slow stages of hauling with the Danish seine), the group of fish in front of the net mouth increased in numbers as the haul progressed, and the concentration extended forward to at least the level of the wing ends. With the flatfish and gurnards the concentration of fish remained at about the height of the groundrope throughout the duration of the haul, but with the roundfish, as their numbers increased they piled upwards as well as forwards and on some occasions the concentration extended above the height of the headline, over which some fish escaped.

(iv) The reactions of the fish were essentially the same when the seine net consisted of only its front part (i.e. without its funnel and bag).

Thus the general pattern of behaviour revealed by these observations in shallow water in daylight was essentially the same as that observed in tanks. Again they suggest that the fish were responding to the visual stimuli generated by the net mouth and the ropes rather than to, for example, acoustic or disturbance stimuli. Similar results were obtained by High and Lusz (1966) when observing the behaviour of small herring inside a pelagic trawl. They report that "Herring were observed maintaining position within the trawl at all points from just inside the mouth to the 'bitter end' of the bag". They also observed fish outside the net approaching it and becoming orientated to it.

Observations on the behaviour of fish in the vicinity of the mouths of trawls in deeper water and in darkness have been made using photographic techniques by Scottish and Canadian workers (Parrish, Blaxter and Dickson, 1962; Beamish, 1966). These workers used still cameras with electronic flash fitted to the square of the trawl, behind the headline, and photographed fish at fixed intervals of time during a haul in the vicinity of the mouth of the net, immediately in front of the groundrope. In the Scottish experiments an exposure was taken every minute, and in the Canadian ones every 12 seconds. Their observations on a number of gadoid and clupeoid species (e.g. cod, haddock, whiting, herring) for hauls made in daylight showed the same type of orientation as that reported above for the tank experiments and for the seine net at sea, the fish being orientated away from the trawl and swimming along with it in front of the groundrope. This suggests that the behaviour pattern and process of capture of these species by the trawl is essentially the same as for the Danish seine. At night, however, in addition to fewer fish being photographed during a haul than in daylight, the orientation of fish along the line of tow and away from the trawl was much less marked. This was particularly the case for cod in Beamish's observations, where "a comparatively high percentage were headed towards the wings or into the mouth of the trawl". While in the Scottish observations the proportion of fish heading along the line of movement of the net was greater than in other directions in darkness as well as in daylight, probably due to the responses of the fish to tactile stimuli produced by the groundrope, the variance of the observations about the mean direction was larger at night than in daylight. In the case of flatfish, Beamish found, in daylight, a much lower degree of orientation along the line of tow of the trawl than for the roundfish species and also little difference between the directions of movement in daylight and darkness. This result for the daylight hauls is somewhat surprising in the light of the observed behaviour of flatfish to the seine net. It is interesting that in the Scottish experiments, despite large numbers caught in some of the hauls, no flatfish were observed in any of the photographs in either daylight or darkness. This would tend to accord with Beamish's observed absence of orientation and movement along the line of tow rather than with an orientated movement and hence accumulation in front of the groundrope.

Springer (1957) made underwater television observations of the reactions of Sardinella anchovia and obtained somewhat similar results to those reported above for gadoids and clupeoids in daylight, although he reported slight changes in swimming speed to avoid parts of the gear. Radakov (1962) also observed concentrations of Clupeonella deliculata and Engraulis encrasicholus swimming without panic and seemingly in an orderly manner in the mouth of a trawl towed at 1.5 knots. In addition to direct observation and photography, information on the behaviour of fish in the vicinity of trawls has also been made by the use of sonar techniques. Schärfe (1955) studied the reactions of herring shoals to German bottom herring trawlers in the North Sea by echosounding from a small boat in the vicinity of the trawl. He observed no marked avoidance responses by the fish to the approaching gear. Extensive studies have also been made of the reactions, especially of herring, to pelagic trawls using netzonde equipment attached to the headline of pelagic trawls. Schärfe (1960) reported that at a towing speed of 3 knots herring swam along with the net in the vicinity of its mouth, but they also showed a tendency to swim downwards on its approach. However, this tendency has not been confirmed by all other workers. For example, Okonski and Konkol (1957) report an upward movement by herring on the approach of a pelagic trawl. It would seem that the behaviour will depend on the level of the fish relative to the net and perhaps also the water conditions, especially the light properties. Mohr (1962) showed from netzonde records that the pattern of behaviour of herring in the vicinity of the mouth of a pelagic trawl varied with their density and also with such physiological factors as maturity stage. In general his observations also showed less reactivity by the fish to the net in darkness than in daylight and, in daylight the echo records indicated a generally orderly pattern of behaviour. Other workers, e.g. Manteufel et al. (1958), report that Baltic herring reacted to the trawl boards, warps and trawl net and to the towing vessel.

4 DISCUSSION

The results of the observations reported above point to the overall importance of visual stimuli in determining the behaviour of fish to moving as well as to stationary gears, under conditions where sight is possible. They suggest that with the towed gear (trawls and seines) in daylight fishing the warp, headline and footrope of the net and the bridles (sweeps) (for trawls) and ropes (for seine nets) together form a herding and collecting function, bringing the fish into the centre of the net's path. However, except for flatfish species, for which direct observations of behaviour in relation to seine net ropes have been made, there are few data on the precise mode of action and efficiency of the bridles and ropes in this function and to what extent their herding properties are the result of responses by the fish to visual as distinct from tactile, vibratory (high and low frequency) or disturbance stimuli. Further study of the nature of the stimuli generated by them (both visual and non-visual) and of the reactions of fish to them, are required. Experiments by Bagenal (1958) comparing the catching capacity of a trawl fished with and without sweeps in both daylight and darkness are of interest in this context. His results were in accord with earlier workers in showing a much higher catch with sweeps than without them, and he found that this applied in both daylight and darkness. Although he made no measurements of the underwater light intensities under his daylight and darkness conditions and took no account of possible differences in the configuration of the mouth of the net (wing spread, headline height, etc.) when used with and without sweeps, he attributed the greater catch with sweeps, especially at night, to the non-visual stimuli generated by them, which herded the fish inwards towards the path of the net. It is well known that most species of fish perceive low frequency sounds and vibratory stimuli and a number of workers have observed fish responses to them, e.g. ship noise (see review by Mohr, 1960), but there are as yet few observations on the nature of the responses (especially their duration and directivity) of fish to the noise and vibratory stimuli generated by trawl sweeps or seine net ropes in the absence of visual ones.

Sounds[1] are generated by different parts of the fishing unit, i.e. ship, warps, trawl boards, bridles and net over a wide range of frequencies (Chapman; this meeting). It is well known that most species of fish perceive sounds over a fairly wide range of frequencies and the results of some tank experiments (e.g. Welsby et al., 1964) have shown avoidance responses to sounds in the lower frequency range (less than 500 cycles/sec.). However, there is still no definite experimental evidence to show that these stimuli play any significant part in determining the behaviour of fish in the vicinity of trawls and other fishing gears during fishing operations in the open sea. The inference of the Scottish experiments in tanks (Blaxter and Parrish, 1966) is that these stimuli are of relatively small importance in eliciting directional, avoidance responses by the fish, yet the results of Bagenal's comparative fishing experiments point to them doing so. Other field observations provide conflicting results. As summarised by Mohr (1960) some authors report marked responses to the noise of ships' engines and to trawls, while others report no marked effect. In general, in cases where responses have been observed, they have usually been short-lived and have tended to be elicited by sudden rather than continuous noises.

An important element of the environment which must not be overlooked in this context is the light produced at night by bioluminescent organisms in the sea. These may, on some occasions, produce sufficient light under the influence of the disturbance caused by the trawl boards, bridles and net of a trawl gear to produce strong visual stimuli.

Although the results reviewed above have already provided a much clearer understanding of the patterns of behaviour and reactions when fish come into contact with fishing gears and hence of some of the principal behavioural factors involved in the capture process, there are still many gaps in our knowledge both of the precise nature of the stimuli which elicit the observed responses and of the characteristics of the responses themselves. It is clear that very little is yet known of the pattern of behaviour in the vicinity of fishing gear and the principal stimuli generating it under non-visual conditions. The results of the Scottish observations in tanks on herring and gadoid species suggest that tactile stimuli are perhaps the most important in eliciting significant responses in darkness, but these results are not supported by field observations by some other workers, which indicate substantial reactions by fish in darkness to the approach of ships and fishing gears. Clearly, more observational work on the reaction of fish to moving objects and fishing gears under non-visual conditions are required to elucidate them. The recently developed sector scanning sonar equipment (Welsby, Blaxter and Chapman, 1963; Welsby et al. 1964; Voglis and Cook, 1966; Cushing and Jones, 1966) should provide a powerful new tool for this purpose, as should direct and photographic observations from manned, underwater vehicles equipped with cine and still, photographic equipment, as indicated by recent Russian work (e.g. Radakov, 1960; Radakov and Solovyev, 1959; Zaitsev and Radakov 1960).

Another factor about which little is currently known is whether fish learn to avoid fishing gear. Some authors have drawn attention to the possibility of conditioned responses being developed following repeated exposure to the stimuli generated by fishing vessels and/or gear, although no convincing evidence of this type of behaviour occurring to any significant extent in existing, exploited fish stocks has been presented. However, a number of workers have shown from aquarium experiments that fish can be conditioned to respond to a number of different stimuli, including acoustic ones, so that the possibility of some conditioned behaviour in species subject to intensive exploitation cannot be ruled out. Clearly, more work on this subject is needed, although in the author's opinion it seems unlikely that learned, avoidance reactions can be of any major significance in exploited, marine fish stocks.

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[1] This is used in a wide sense to include vibratory and disturbance stimuli from the very low frequencies (a few cycles per second) up to ultrasonic frequencies.

It is clear that more observational and experimental work is required on the behaviour of fish in the vicinity of fishing gear, on the types of stimuli (and their intensities) which the whole fishing unit and its different components generate, and of their respective importance in generating the observed patterns of behaviour. Only in this way will it be possible in gear design and operation to optimise, rationally, the physical properties of the gear and the fishing operation.

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SOUND RECEPTION IN TELEOST FISHES IN RELATION TO THE SOUND SOURCE DISTANCE

by

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Abstract

Particle displacement is not determined by the signal strength of the source and the distance from it according to a simple inverse square law. There is a so-called acoustic near-field the size of which is frequency dependent. The variation of auditory thresholds of fish must be considered in relation to the extent of this acoustic near-field. The near-field effect is negligible beyond one wavelength. Experiments have shown that the existence of a swimbladder is essential for hearing by fish beyond the acoustic near-field. The noise from fishing vessels and gear can probably be detected at a considerable distance by fish with swimbladders. In the acoustic near-field the lateral line acts as a receptor so that even fish without a swimbladder are sensitive to sonic and infrasonic sounds of long wavelength.

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RECEPCION DEL SONIDO POR LOS PECES TELEOSTEOS EN RELACION CON LA DISTANCIA DEL ORIGEN DE AQUEL

Extracto

El desplazamiento de las partículas no está determinado por la intensidad de la señal del origen y por la distancia de ella según la simple ley del inverso del cuadrado. Existe un llamado campo acústico próximo cuya extensión depende de la frecuencia. La variación de los umbrales de audición de los peces se debe considerar en relación con la amplitud de este campo acústico próximo. Más allá de una longitud de onda el efecto del campo próximo es insignificante. Los experimentos han demostrado que es esencial la existencia de una vejiga natatoria para que el pez pueda oir pasado el campo acústico próximo. El ruido producido por las embarcaciones y los artes pesqueros probablemente pueden detectarlo los peces dotados de vejigas natatorias a una distancia considerable. En el campo acústico próximo la línea lateral actúa como receptor, de forma que incluso los peces que carecen de vejiga natatoria perciben las vibraciones sónicas e infrasónicas de longitud de onda larga.

RECEPTION DES SONS CHEZ LES POISSONS TELEOSTEENS SELON L'ELOIGNEMENT DE LA SOURCE SONORE

Résumé

Le déplacement des particules au passage de l'onde sonore n'est pas déterminé uniquement par la puissance du signal émis par la source ni par la distance de celle-ci (conformément à la simple loi de l'inverse du carré de la distance). Il existe une zone dite "champ proche acoustique", dont l'étendue varie en fonction de la fréquence. Les variations des seuils d'audibilité du poisson doivent être étudiées en tenant compte de la taille de ce champ proche acoustique. A une distance supérieure à une longueur d'onde, l'effet de champ proche devient négligeable. Les expériences ont révélé que la présence chez le poisson d'une vessie gazeuse est indispensable à l'audition au-delà du "champ proche". Les poissons dotés d'une vessie gazeuse peuvent probablement détecter à une distance considérable le bruit produit par les bateaux et les engins de pêche. Dans le champ proche acoustique, la ligne latérale intervient comme récepteur, de sorte que même les poissons sans vessie gazeuse sont sensibles aux sons et infrasons à grande longueur d'onde.

1 INTRODUCTION

In determinations of auditory thresholds in fish, sound pressure has been the commonly used reference parameter. But Enger (1966) found that the sound pressure threshold in goldfish varies with the distance of the fish from the sound source. Thus, for a sound frequency of 50 Hz, the threshold difference was 30 db (decibel) when the distance between the fish and the underwater loudspeaker varied from 0.2 to 2.0 m. For increasing sound frequencies the threshold difference became gradually lower and for frequencies above 700 Hz no difference could be detected at the two distances mentioned.

The variation in auditory thresholds with changes in distance is due to the effect of the acoustic near-field, delineated by Harris and van Bergeijk (1962), Harris (1964) and van Bergeijk (1964), who found that the particle displacement produced by sound is determined by the sound pressure as well as by the distance from the sound source, according to the formula:

$$d = \frac{p}{2\pi f \rho c}\left[1 + \left(\frac{\lambda}{2\pi r}\right)^2\right]^{\frac{1}{2}}$$

where d = particle displacement, p = sound pressure, f = sound frequency, λ = wavelength of sound, ρ = density of water, c = sound velocity, r = distance from the sound source.

From the formula it can be seen that for a given wavelength and sound pressure the displacement amplitude varies in inverse relation to the distance from sound source. When the distance is larger than one wavelength the near-field effect becomes negligible. For 1000 Hz, the wavelength is 1.5 m, for 100 Hz it is 15 m and for 10 Hz it is 150 m.

Since studies of hearing in fish have mostly been performed in relatively small tanks, the results apply mainly to the effect of the acoustic near-field. Studies on sound reception of teleost fishes in the far-field (reception of propagated sound waves) were virtually lacking, until the experiments of Enger and Andersen (1967). The swimbladder is known to contribute to the sensitivity of high frequency sound perception in some freshwater species (Ostariophysi) which possess Weberian ossicles connecting the swimbladder with the labyrinth (Kleerekoper and Roggenkamp, 1959). The role of the swimbladder as an accessory auditory organ in fish generally, however, has been postulated only from hypothetical considerations (van Bergeijk, 1964; Alexander, 1966).

2 EXPERIMENTS

To elucidate the role of the swimbladder in hearing, Enger and Andersen (1967) experimented with two species of fish, namely codfish (Gadus morhua) which has a swimbladder, and sculpin (Cottus scorpius) which has none. The experiments consisted of recording saccular microphonic potentials from the fish ear through implanted electrodes, while the fish was kept in a small open mesh cage hanging from a rowboat anchored at various distances of up to 10 m from an underwater loudspeaker. Sinusoidal sound stimuli were delivered through an underwater loudspeaker hanging from a quay and facing an open stretch of more than 2 km of a deep fiord.

The results obtained were strikingly different in the two species. Figure 1A and B show records of microphonic potentials in cod and sculpin, respectively. It is seen

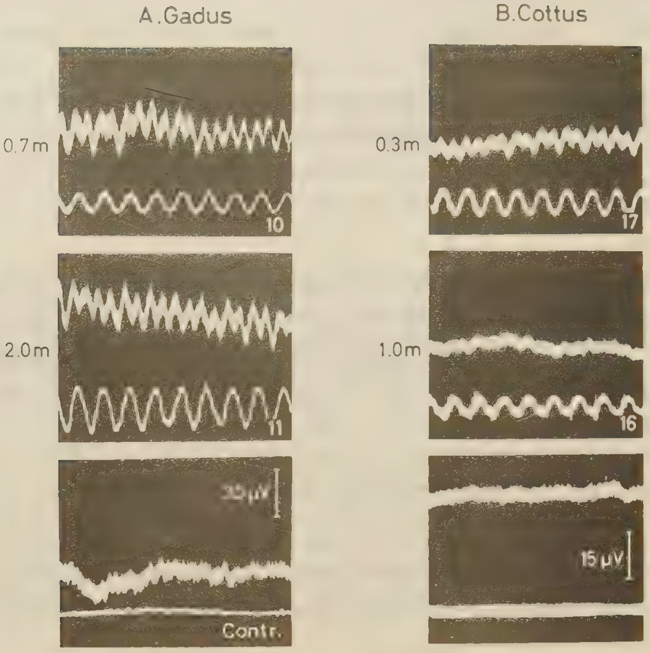

Fig. 1 Microphonic potentials recorded at two different distances (given on records) between fish and loudspeaker.
A. Codfish, 400 Hz
B. Sculpin, 200 Hz

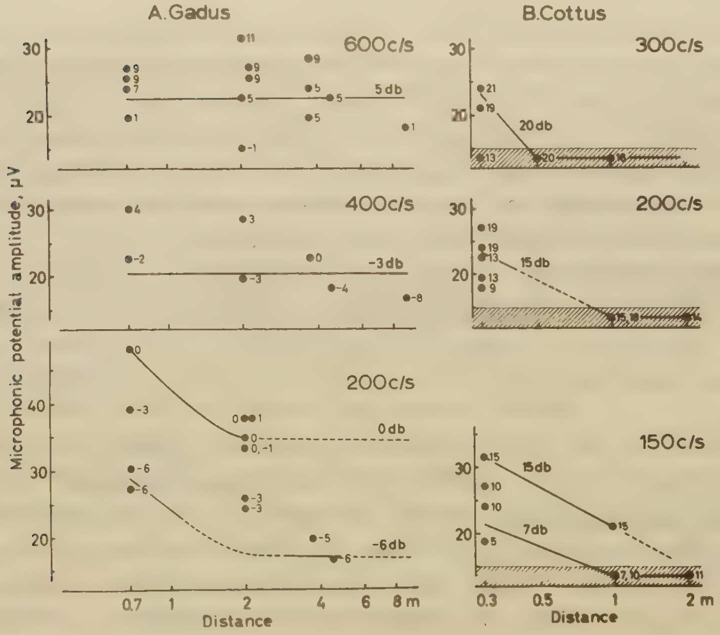

Fig. 2 Amplitude of microphonic potentials at different distances between fish and underwater loudspeaker. Sound pressures (in db) given for each point and each curve, sound frequency for each graph.
A. Codfish B. Sculpin.
Hatched area in B represents background (electrical) noise level

that in cod, the potential amplitude is the same at 0.7 and 2.0 m distances for constant sound pressure. In the sculpin, however, the potential amplitude changed with both the sound pressure and distance. In Fig. 2A are plotted the amplitudes of the microphonic potentials for three different sound frequencies at various distances between the loudspeaker and the codfish. Except for the low sound frequency of 200 Hz the response amplitude is clearly dependent on the sound pressure only and not on the distance to the sound source. For these frequencies (400 Hz and higher) the fish is not within the near-field at 0.7 m distance. For 200 Hz at 0.7 m, however, an effect of the acoustic near-field was observed. In the sculpin (Fig. 2B), on the other hand, no microphonic potentials were recorded when the fish was beyond the acoustic near-field. For frequencies above 150 Hz no responses whatsoever were recorded at distances beyond 1 m.

3 CONCLUSIONS

The above observations indicate that the swimbladder is essential to teleosts, for hearing propagated sound waves in the acoustic far-field. The swimbladder undergoes volume changes due to pressure changes caused by the passage of sound, and these volume changes in turn displace the surrounding tissue and thereby also the auditory receptors. The swimbladder functions as a transducer transforming pressure into displacement and it seems justified to conclude that displacement is a better parameter for determining auditory thresholds than acoustic pressure (Harris and van Bergeijk 1962, Olsen 1965 MS, Enger 1966).

The auditory thresholds of many marine species are so low (Tavolga and Wodinsky 1963, Enger 1967) that the noise from fishing vessels and gear can probably be detected at a considerable distance by fish possessing swimbladder.

The acoustic near-field effect does also stimulate receptors of the lateral line organ (Harris and van Bergeijk, 1962) which are sensitive to sonic as well as infrasonic frequencies. This implies that also fish without swimbladder can detect low-frequency sound source at a long distance. The noise from ships (and trawl) has its acoustic energy maximum for low frequencies below 100 Hz (a considerable peak even below 10 Hz). The near-field of such sound sources, therefore, may extend for more than 100 m (λ = 150 m for 10 Hz), and a fish, through its lateral line organ, may even be able to detect the direction of the sound source at fairly long range.

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SCUBA DIVING, A VALUABLE TOOL FOR INVESTIGATING THE BEHAVIOR OF FISH WITHIN THE INFLUENCE OF FISHING GEAR

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Abstract

The use of scuba diving methods in the study and documentation of trawl and fish behavior are discussed. Numerous underwater observations of flatfish, roundfish, and other marine animals within the influence of capturing gear have been made. Some limitations and potential hazards pertinent to the use of scuba diving near trawls are discussed.

E/2

LE SCAPHANDRE AUTONOME, PRECIEUX INSTRUMENT POUR L'ETUDE DU COMPORTEMENT DU POISSON DANS LE RAYON D'ACTION DES ENGINS DE PECHE

Résumé

La communication examine l'emploi du scaphandre autonome pour l'étude et le rassemblement de données sur le comportement du chalut et du poisson. Cet appareil a permis de rassembler de nombreuses observations sous-marines sur les poissons, notamment les poissons plats, et autres animaux marins se trouvant dans la zone d'action des engins de pêche. L'auteur fait également état de certaines limitations de la méthode ainsi que des dangers que peut présenter la plongée à proximité de chaluts en marche.

LOS BUZOS AUTONOMOS, INSTRUMENTOS VALIOSOS PARA INVESTIGAR EL COMPORTAMIENTO DE LOS PECES DENTRO DE LA ZONA DE INFLUENCIA DE LOS ARTES DE PESCA

Extracto

Se examina el empleo de los buzos autónomos en el estudio y documentación de la pesca al arrastre y del comportamiento de los peces. Se han realizado numerosas observaciones submarinas sobre los peces planos, peces de fondo y otros animales marinos que se hallan dentro de la influencia de los artes de captura. Se examinan igualmente algunas de las limitaciones y riesgos potenciales que existen cuando los buzos autónomos trabajan cerca de los artes de pesca al arrastre.

1 INTRODUCTION

Man's attempt to conquer the oceans has been greatly aided by the development of scuba (self-contained underwater breathing apparatus) diving equipment. The basic equipment was available in the early 1950's but its value to fishery scientists was not generally recognised until after 1955. Even then few researchers seized the opportunity to descend beneath the water surface to see first hand what took place.

Now, as aquanauts swim free at depths to 1,000 ft and many sportsmen dive deeper than 150 ft for pleasure, fishery scientists will certainly increase their use of this valuable research tool. A classic example of the information gathered by scuba divers is the cine film of nets in action prepared by the Marine Laboratory, Aberdeen, U.K.

During the past 12 years, U.S. scientists have utilized scuba techniques to investigate numerous problems. Underwater biologists of the California Department of Fish and Game made extensive surveys to determine the effectiveness of various materials for construction of artificial fish reefs, University of Miami researchers have studied ecology of reef fish, and the Bureau of Commercial Fisheries has used divers to evaluate nets and observe the reactions of fish to capturing gear.

Scuba diving has been a successful tool employed by the Bureau of Commercial Fisheries since 1955 and at the Exploratory Fishing and Gear Research Base, Seattle, Washington, since 1958. This technique is only one approach to the overall program of gear development and fish behavior studies, yet it has provided information not otherwise available.

At the Base in Seattle, training qualified fishery scientists to use scuba gear was more practical than to rely on commercial divers who may not understand the full meaning of what they see. The present diving team has two fishery biologists and one electronic engineer, all specializing in gear development. Other staff members have participated in the earlier studies; therefore, they can understand underwater photos and reports prepared by the diving team.

2 TECHNIQUES

Initially, diving observations were carried out from a sea sled towed adjacent to the trawl (Sand, 1956). This restricted the effectiveness because a diver had to return to the surface to order tow rope length adjustments each time a different part of the net was to be observed, and divers could not follow the activities of a particular fish. Midwater trawls were too large to be fully inspected on one dive.

When observations showed most nets to be stable and taut (much like an airport wind sock), divers began working directly on the net (High and Lusz, 1965). In early direct contact diving operations, a small line was tied to a surface float and the trawl wing tip to lead the divers to the net. A power skiff transported the diving team to the vicinity of the surface floats. They departed from the skiff in the path of oncoming floats. As a wing tip float passed by, each diver seized the line and descended hand over hand to the trawl. The skiff then maintained a course parallel to the trawl, ready to pick up the divers when they surfaced.

The method of descending to a trawl is now accomplished by entering the water from the fishing vessel and moving down the towing warps (Fig.1). In this way, a minimum of energy and compressed air is expended. Caution must be observed as the divers approach the otterboards, especially when the boards are in contact with the bottom. Clouds of mud obscure the sweeplines between the otterboard and the net so that the diver must feel his way along the sweepline to the net where it is usually less turbid.

When observing a midwater trawl being towed at speeds up to about 2.5 kn divers can conveniently move hand over hand to all parts of the net.

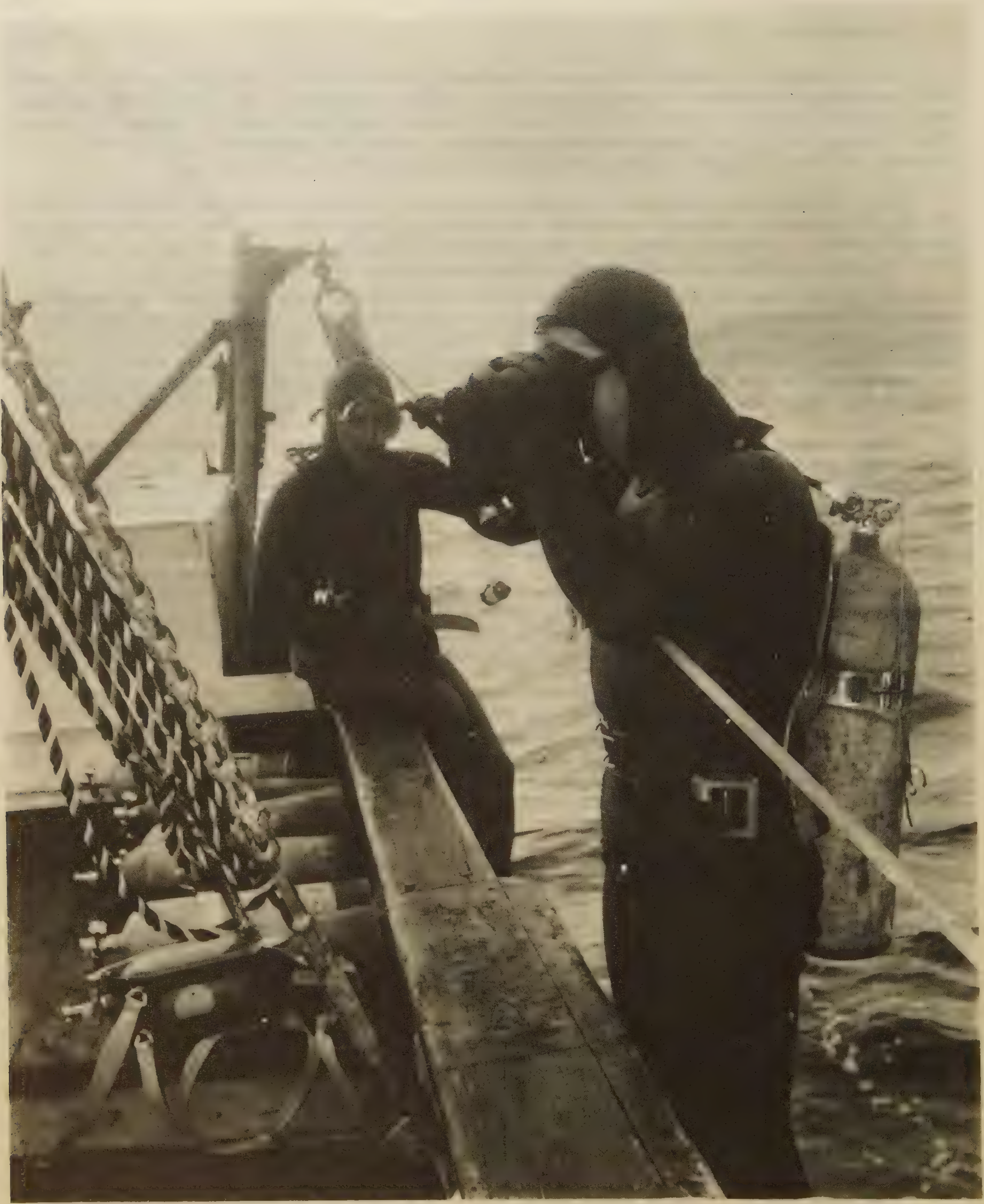

Fig. 1 Diving scientists prepare to jump from the side of a stern trawler and follow the towing warp down past the otterboard to the net

2.1 Underwater photography

Using pressure-proof cameras, divers move freely to all parts of a trawl, both inside and out, and take photographs that are a major addition to underwater observations. They often follow and photograph the movements of a single fish from the time it comes within the influence of the trawl until it reaches the cod end.

Observers wishing to study segments of a total fish response can do so by stopping action with a strobe camera for later detailed study. A camera instantly records occurrences that would take several minutes to write underwater. A permanent picture record also permits other scientists to see what has taken place.

Our divers use both cine and still cameras. One 35-mm camera has an electronic flash and permits 36 exposures on one dive.

Low light levels in deep water and turbidity caused by gear on the bottom sometimes restrict photographic success. Artificial light from strobe or flash bulb will reflect from plankton or debris suspended in the water and create back scatter. This produces a fog-like appearance on the film.

3 FISH REACTIONS TO TRAWLS

On many occasions Bureau divers have observed fish reacting to trawls. Herring, smelt, squid, rockfish, and bottomfish have been observed and their different reactions to trawls noted. It is hoped that these observations will assist fishermen and gear technologists to design more effective trawls.

3.1 Midwater trawls

Several fish species have been observed for various time periods in midwater trawls. Usually some fish were in the net when the divers arrived. Those fish, which the divers saw pass into the large net mouth (as much as 50 ft by 60 ft), did not display signs of distress. Individuals or groups oriented to the web and maintained their position facing the apparent current (Fig. 2). I must mention, to a surface observer the trawl appears to move through a stationary column of water. However, the divers who hold on to the net and the fish in it view the situation as a stationary net in a current of water. For the purpose of this paper, the diver's perspective will be used.

The following observations were made on small fish shoals found in the protected waters of Puget Sound, Washington.

3.1.1 Herring and smelt Those fish, especially herring (Clupea pallasii) and smelt (Hypomesus pretiosus), which entered the net first, often moved back to just ahead of the cod end where they assumed a stable swimming position. Late-arriving individuals would not crowd back but took up a position farther forward. As long as the fish could maintain their position, the net continued to fill forward until fish were scattered throughout the length of the net. As individuals became tired, they slowly dropped back to the bitter end of the bag. Those fish whose tails touched the netting surged ahead a few feet if strength permitted.

The observed herring and smelt were small enough to escape through the 3-in meshes. However, most would swim for periods up to 20 min or more without attempting to pass through the netting (High and Lusz, 1966).

The divers could readily approach within a foot or two of the fish, but any sudden motion would usually cause herring to scatter in all directions through the meshes. Visual observations and study of photographs suggest that the herring turned on one side to pass through the top panels of the trawl (Fig.3).

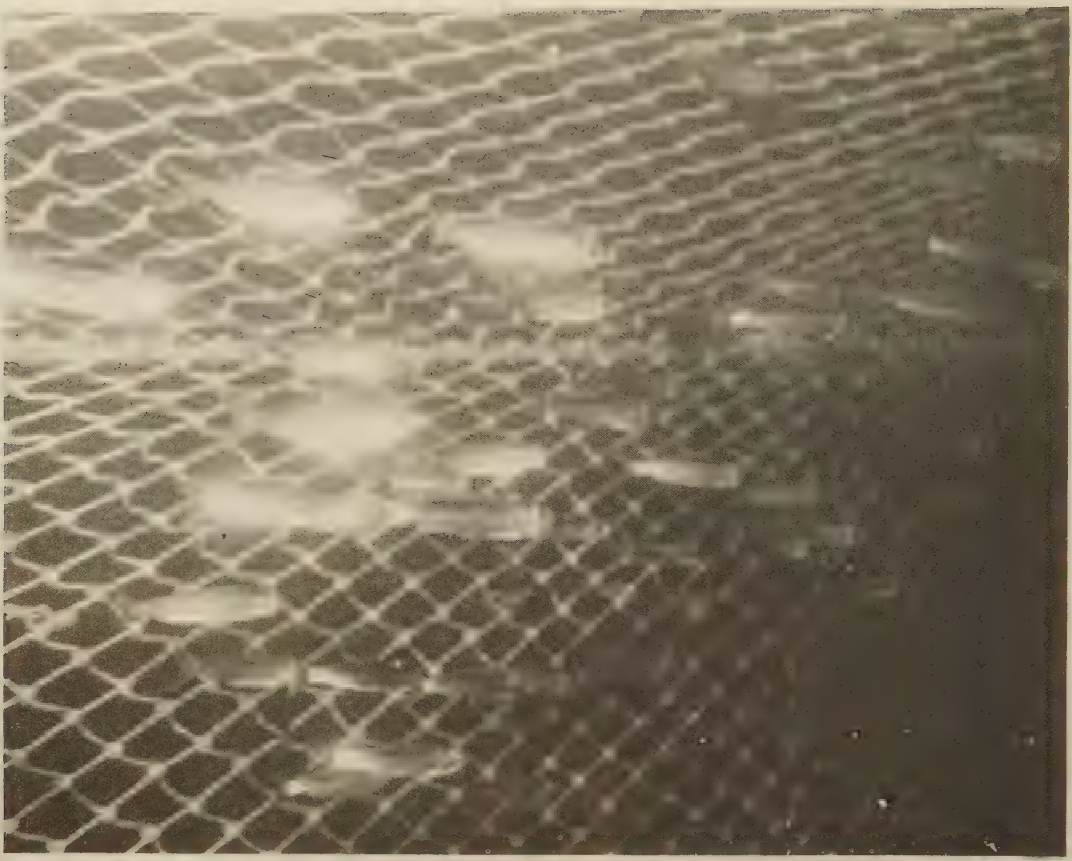

Fig. 2 Six-inch-long herring, inside a trawl, orient to a section of cod end web and swim for long periods. The photographer could slowly move to within 2 ft of the herring without disturbing their position.

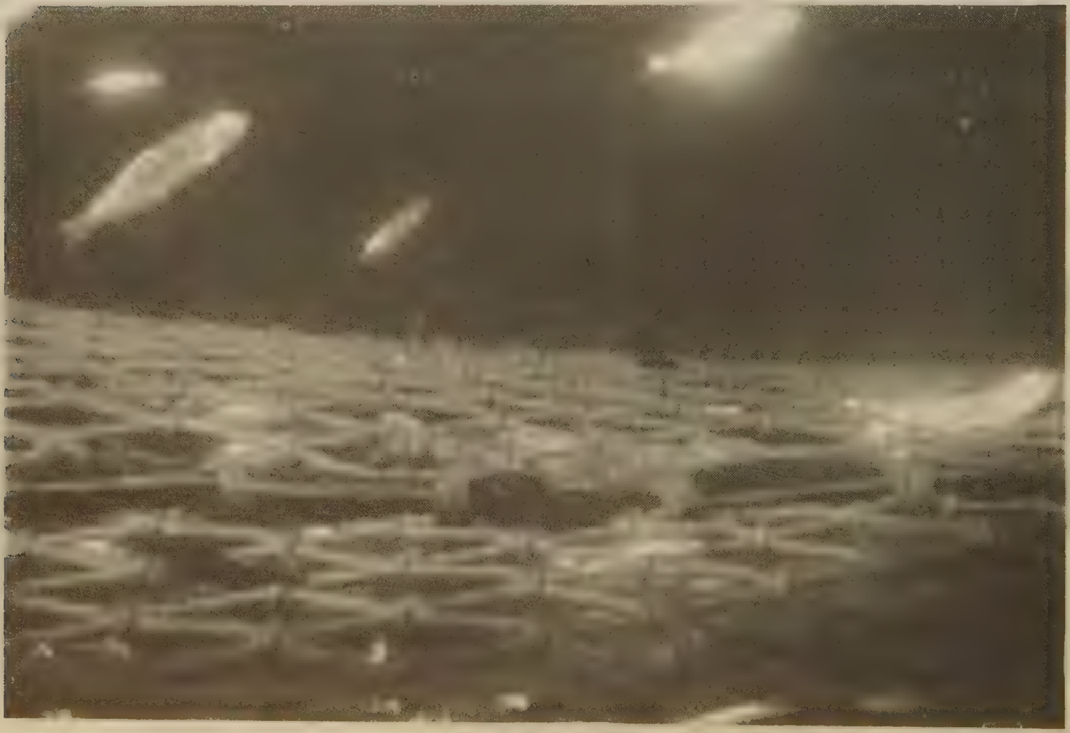

Fig. 3 Underwater view from outside a trawl cod end as herring escape through the meshes. One herring is shown turned on its side to pass through the web

During two observation periods herring schools outside the net approached and oriented to the netting. Individuals broke from the outside school and swam through the meshes into the net to join those within.

3.1.2 Squid Small squid (Loligo opalescens) up to about 10 in total length have been seen on occasion in a midwater trawl swimming among herring (Fig.4). The water flow was probably in excess of 2 kn yet the squid maintained their position for at least 10 min. None of the squid were seen to escape through the 3-in meshes; however, only a few were captured.

3.1.3 Sticklebacks During one cruise the echo sounder detected a fish school 10 fm beneath the surface. A pelagic trawl was set and two divers descended to observe fish reactions to the net. Thousands of 3-in-long, three-spine sticklebacks (Gasterosteus aculeatus) were seen passing into the net. They could not evade the web moving at about 1.8 kn. Many struck netting threads and became wrapped around the twine. Some were affixed in this manner to the net for a minute or more. As they broke loose they drifted away. Most eventually passed through the cod-end meshes.

3.2 Bottom trawls

Observations on bottom trawls by divers were more difficult because of the mud stirred up by the otterboards, sweeplines, and groundrope. The leading edge of components touching bottom was easy to see. When the vessel made a gentle starboard turn, the port portion of the trawl was often free of mud stirred up by the port otterboard and sweepline.

Flounders and near-bottom fish species usually did not react to cable sweeplines or otterboards until the object was very close or actually touching the fish (Fig. 5). Sweeplines between the otterboard and net were seen herding fish, but the fish reacted less quickly after the cable or footrope had overtaken them a few times.

Recently observations were made of a 400-mesh eastern bottom trawl rigged by a commercial fisherman to be most efficient for flounders. Fishes were herded by the sweeplines and forward net wings, which were in contact with the bottom. However, the centre of the footrope was 10 in off the bottom (Fig. 6) permitting a large percentage of the flounders to pass beneath the net.

Divers seldom see flounders rise more than 3 ft off the bottom when disturbed by a trawl, indicating, as might be expected, that a high opening net is of questionable value for these species (Fig. 7). Roundfish, on the other hand, had a greater vertical movement and were seen to rise 5 to 10 ft above the footrope. Neither roundfish nor flatfish resting on or near the bottom was seen to react to a trawl headrope overhang if it passed at a height of 10 ft or more above the fish. Once flounders passed well aft of the footrope, they usually drifted quickly to the cod end facing the direction of the tow. Roundfish more often oriented to a section of web and swam with the net. Some then turned and swam across to the other side panel but were eventually carried back toward the cod end. With small catches, individuals of all species swam for long periods in the cod end because of the very low water velocity.

Fishermen often evaluate net contact on bottom by the amount of miscellaneous bottom trash that is captured or because cable and chain footrope are rubbed bright. Turbulence behind otterboards has been observed to move trash high enough off bottom so that the trash was carried into the net 15 to 30 fm behind. Also, when only a small part of the net touched bottom, many varieties of bottom life were carried into the net.

4 OBSERVATIONS OF FISH IN THEIR NATURAL HABITAT

Bureau of Commercial Fisheries divers have observed salmon, rockfish and anchovies in their natural habitat. These fishes were observed reacting to each other, divers, baited hooks, predators, and tidal currents.

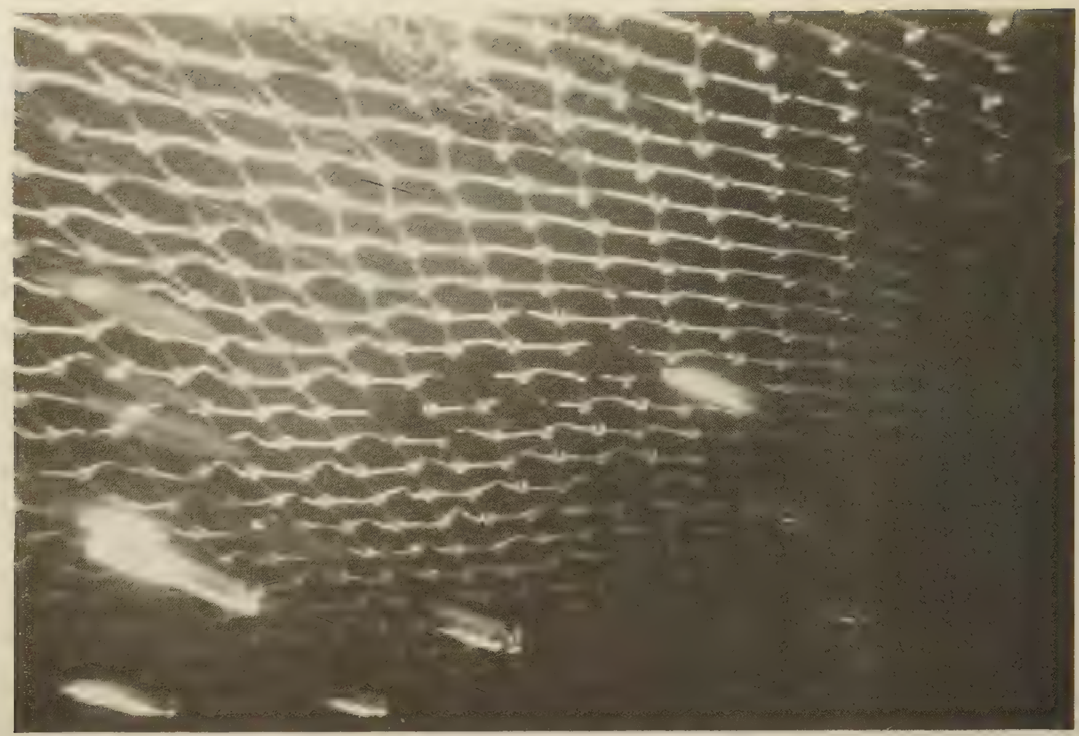

Fig. 4 Small squid may be seen in the left center of the picture swimming with herring at about 2 kn inside a trawl cod end

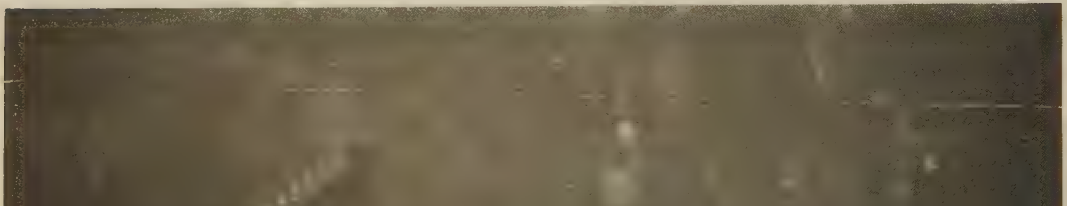

Fig. 5 An underwater view of a trawl tickler chain as it approaches within a few inches of a flounder resting on the bottom. A flounder in the background can be seen swimming over the top of the chain.

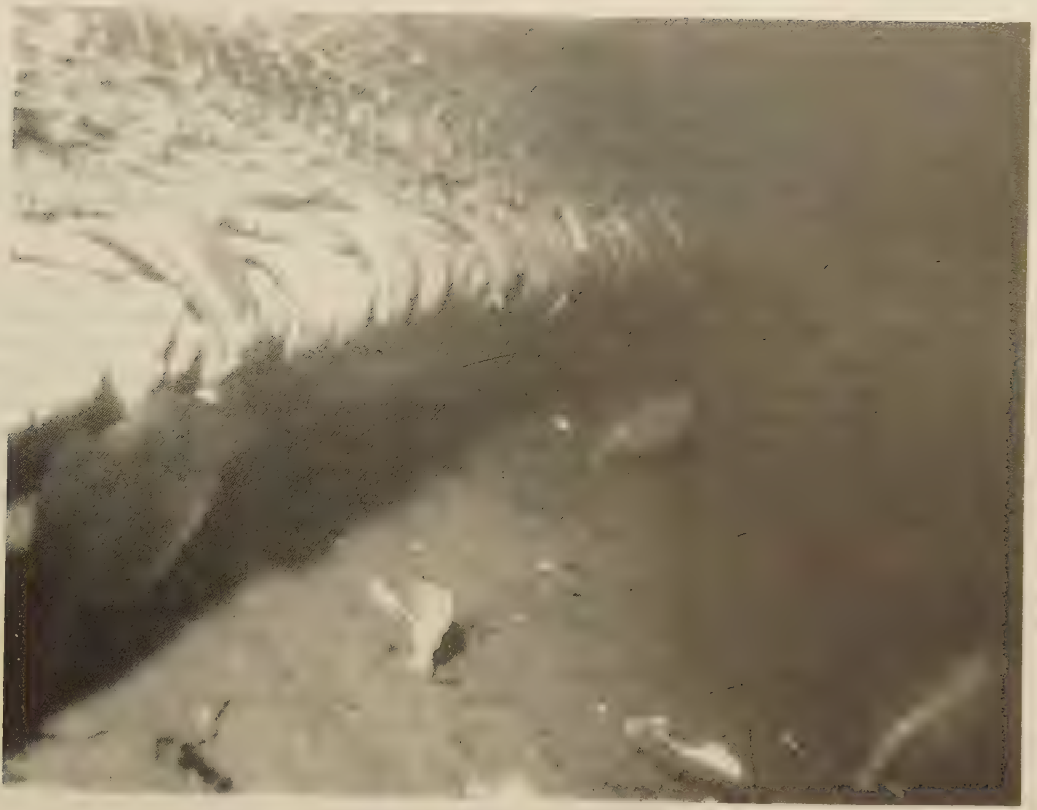

Fig. 6 This bottom trawl footrope passes 10 in above the bottom, permitting numerous fish to escape beneath the trawl. Several marine invertebrates can be seen protruding from the sand.

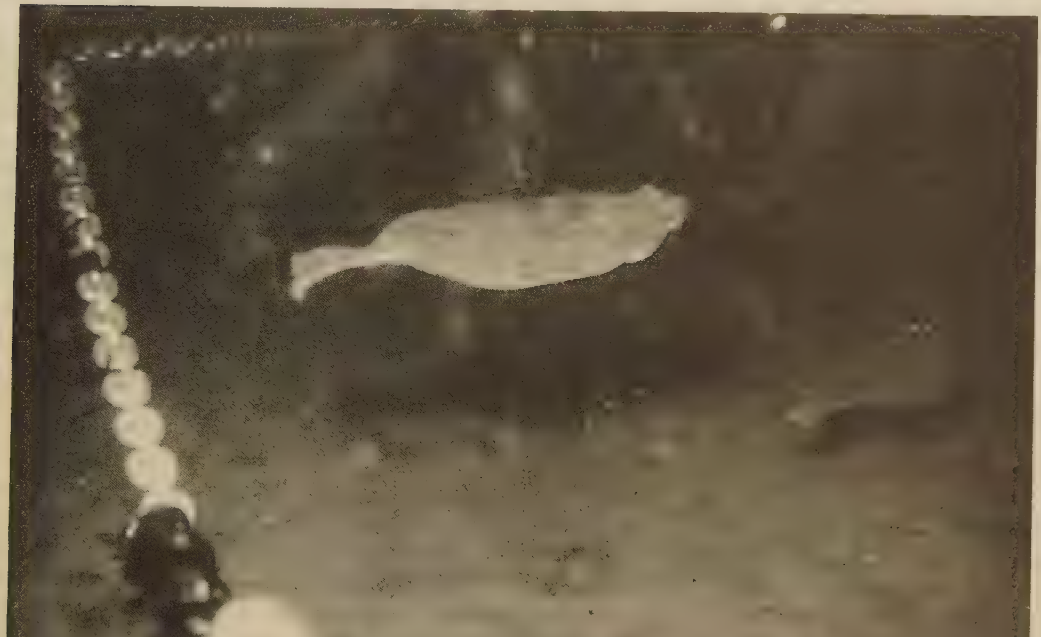

Fig. 7 Two flounders swim 3 to 10 in off bottom ahead of a trawl tickler chain. Both fish settled on the bottom about 20 ft ahead of the net until the moving chain again disturbed them

4.1 Salmon

Salmon (*Oncorhynchus* spp.) are the only North Pacific marine fish species encountered which are easily frightened by divers. Divers seldom see salmon in their natural environment, which leads divers to believe salmon can detect the diver's presence at some distance.

4.2 Rockfishes

Various rockfish (*Sebastodes* spp.) react to the influence of tidal currents in a manner that may affect their chances of capture. On several occasions while diving over a smooth bottom at slack tide, rockfish have been seen randomly distributed or gathered about small objects such as a rock or piece of rotted wood. As the tidal current increased, schools up to several hundred individuals were observed. Each fish was facing into the current while either hovering a few inches above the sand or actually resting on the bottom; however, the forming of such schools was not actually seen. Considerable diver activity, including spearing the larger schooled fish, did not cause them to disperse.

Black sea-bass (*Sebastodes melanops*) commonly form large schools adjacent to steep underwater rock walls or above rocky bottom. During strong tidal currents, the fish usually swim into rocky crevasses or rest on their pectoral fins on the lee side of a ledge. As the tide slackens, the school reforms up and away from the rocks.

4.3 Response to baited hooks

Fish response to a baited hook can be easily observed under natural conditions in the North Pacific area because most fish ignore a slow moving or stationary diver. On one occasion while diving, I came upon a man in a small skiff fishing with a rod, reel, and baited hook. A large school of sea perch (Embiotocidae) was milling around and feeding on piling barnacles 20 ft below the boat. All the fish remained 5 ft or more off the bottom in a school about 10 ft thick. The fisherman's baited hook was seen as it sank down through the fish to the bottom. Several fish followed the bait but it usually descended through the school before any perch could strike it. No perch swam down beyond the school even though the bait was quite visible. The same response was noted as the bait was retrieved up through the school to the surface. The fisherman's catch rate was very low considering the number of fish present. I surfaced to advise the man of the observed behavior and recommended that the bait be kept within the school depth range. As expected, perch were then hooked as fast as the fisherman could handle them. When the bait stopped within the school, several fish darted to it to either nibble or feint feeding lunges. This action stimulated others to participate until one would rush in, grasp the bait and become hooked. None of the schooled fish were frightened by the erratic actions of the hooked fish or the presence of a diver. In fact, they seemed to be stimulated to search around for other food particles. Some fish followed the hooked individual nearly to the surface.

4.4 Anchovy school

During an underwater filming expedition to British Honduras, a group of divers encountered several large schools of anchovy. Exceptional water clarity permitted the divers to see anchovy react to predation by other species and to the divers themselves. Large predator fish were seen and photographed as they swam along the school perimeter. Occasionally they would dart into the living wall of anchovies. Only those anchovies near the point of attack scattered and then, as though in a single wave, the school parted and let the predator pass.

When the divers descended through the school to the ocean floor 135 ft below, the anchovies parted as the divers passed through, then closed over above them. Soon all surface light was completely blocked out and the divers could see only a short distance with their powerful lights when among the fish. Those divers watching from above observed the anchovies separate as the scuba air bubbles rose through the fish, then again the spot was occupied by the anchovy school. The school as a whole did not appear to respond to activity at a single part of the school.

5 WATER FLOW IN AND AROUND A TRAWL

One facet to a study of fish behavior within the influence of gear is to define the water flow patterns in and around a trawl. Slow-moving water or back eddies within the net could permit fish to rest and renew escape attempts.

During early diving activities the divers had difficulty hanging on to the headrope of a fast-moving trawl but almost no effort was needed to hold on at the bitter end. Web in the forward parts of the trawl was taut from internal water pressure, whereas the after cod end was collapsed with little evidence of water flow. Bottom trash in the cod end was seen to drift in a circular pattern and even be carried forward several feet by an apparent back eddy. Because dives were made in and around the trawls, it was decided to obtain a series of flow readings at various parts of the net.

We rigged a Japanese manufactured T.S.flow meter* for hand-held underwater use (High, Lusz, 1966). The meter was directed into the current at arms length in front of the diver located at the net. The number of meter propeller revolutions were recorded during three 1 min periods, averaged, and the speed calculated by a formula. The data indicated that the speed of water inside the net was about equal to that on the outer side. Although some error was inherent in the procedure, it provided better data than was previously available.

Higo (1964) conducted flow tests in and near model nets, using a thermistor-type current meter. He concluded that the current velocity inside a trawl was mostly equal to or somewhat faster than those at the net mouth and the outer surface of the net.

In 1966, a U.S. manufactured Marine Advisor's Ducted Water Flow System, Model Q-8* was fitted into a waterproof housing for use by divers. The self-contained electronic unit provided a direct reading meter calibrated in knots and feet per second. The ducted impeller transmitted a signal through waterproof cable and fittings to the meter.

Two divers were needed to take a series of measurements. One diver monitored the readout dial as the second operator positioned the probe. Each reading was taken 24 to 30 in away from the netting and ahead of the divers holding on to the net. The probe was positioned into the current, then slowly moved about to encounter the maximum flow. The peak reading was recorded.

Small holes were cut in the web to permit the probe to be extended into the net. Because of the adverse working conditions for divers, including 8°C (46°F) water temperature, limited air supply, and fatigue from hanging on to the net and recording equipment in a strong current, only about 10 stations could be checked on one dive (Fig. 8).

Attempts were made to duplicate conditions among drags; however, these were not completely successful. For example, position one readings (Table I) varied 0.2 kn on drag numbers 1 and 2, even though vessel propeller revolutions were the same and tow cable tension was similar for the two drags. Changing tidal conditions and wind velocities may have affected the vessel.

Position one is designated as the speed of the entire system through the water. The reading was made on the trawl tow cable ahead of the net and otterboard influence and 10 to 15 fm beneath the surface, to reduce the influence of surface tide and wind-caused currents.

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* Use of brand name does not imply endorsement

TABLE I

Water velocity readings in knots, taken at various points outside and inside a midwater trawl

Vessel rpm	Cable tension (lb)	Dive No.	Impellor Position	Sampling Station Number									
				1	2	3	4	5	6	7	8	9	10
320	6,700	1	Outside	1.60	1.80	1.85	1.70	1.55	1.60	1.70	1.50	1.05	0.75
			Inside	--	1.80	1.80	1.85	1.85	1.90	2.00	1.80	1.30	--
320	6,650	2	Outside	1.80	2.10	1.80	2.20	1.75	1.75	1.85	1.65	--	--
			Inside	--	--	1.75	2.15	2.10	1.95	1.95	1.95	--	--
320	--	4	Outside	1.90	2.60	2.15	2.10	1.80	1.80	1.90	1.70	1.80	1.10
			Inside	--	2.50	2.30	2.30	2.00	1.95	1.95	2.05	1.90	0.80
280	5,550	3	Outside	1.50	2.00	1.60	1.60	1.55	1.45	1.55	1.45	1.50	--
			Inside	--	1.60	1.65	1.65	1.70	1.70	1.70	1.80	1.40	--

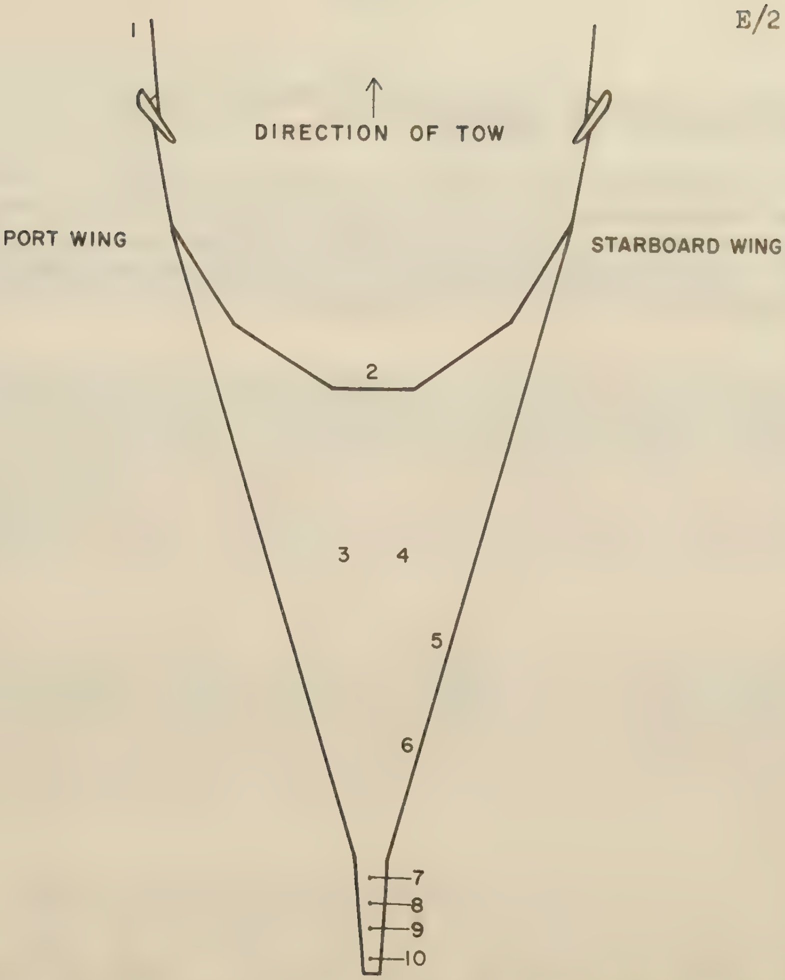
1
DIRECTION OF TOW
PORT WING
STARBOARD WING
2
3
4
5
6
7
8
9
10

Fig. 8 Current meter stations on the top panel of a midwater trawl

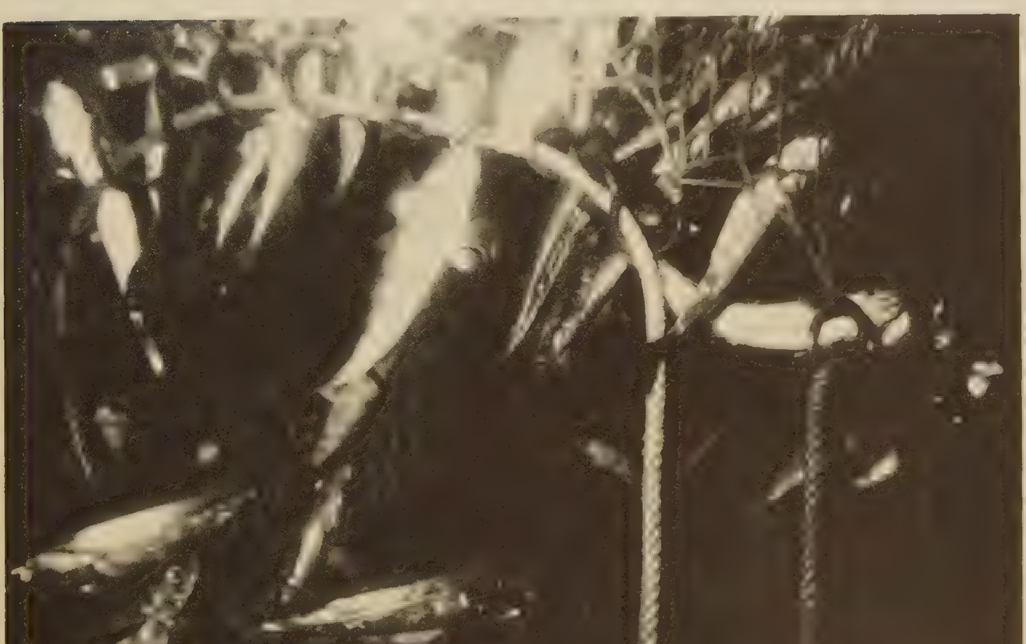

Fig. 9 Hake remain in the cod end after the puckering line has been released, indicating lack of water flow through cod end

It is apparent that the water flow near the web inside the 3-in mesh trawl exceeded adjacent water on the outside.

Water flow measurements taken when herring were in the net indicate that the fish were maintaining their position in flows over 2 kn for 20 min. Other species, including both adult and juvenile (7 to 9 in) salmon, have been viewed maintaining their position inside a trawl at speeds of about 2.1 kn for several minutes. When frightened by the divers, some of the fish would surge ahead out of sight toward the mouth of the trawl.

Reduced water flow in a trawl cod end was demonstrated when divers attempted to release a 15,000-lb catch under water. The divers released the puckering string while the trawl was being towed 12 fm below the surface. Instead of fish bursting out, only a few drifted free as divers pulled the bag open (Fig. 9). The bag was held open while one diver reached inside to pull fish out and another diver shook the bag. It took about 10 min for the fish, which were nearly lifeless, to drift out of the open cod end.

6 LIMITATIONS OF SCUBA DIVING

Diving within the influence of trawl gear to study fish behavior is strenuous and potentially dangerous. A careless diver can become trapped in slack web or possibly be carried into the net. Divers should be well trained gear experts so they will know where they are in relation to any part of the trawl at all times, even when only a small portion of the net is visible in turbid waters. Good physical condition is required to hold on to the net or move from one location to another at towing speeds over 2 kn.

Some restrictions are placed upon diving by the physiological aspects. Nitrogen narcosis can dull a diver's mind and reactions beyond about 150 ft deep. Rapid movement through cold waters (about 7°C to 10°C in the Seattle area) will quickly chill a diver and reduce his effectiveness. Bends may develop after only short stays in moderate depths. Consequently, to make direct observations of fish within the influence of gear is not practical at depths much greater than 175 ft. Work is usually limited to less than 135 ft to permit several dives in one day.

In many regions it is difficult to find waters suitable for divers to observe fish and moving trawls. When working in turbid waters divers have little time to react to a dangerous situation. The water surface must be relatively calm so the divers will be seen upon their return to the surface. The bottom must be smooth to prevent snagging of trawl gear and possible injury to divers.

Scientists who plan to dive near fishing gear should make several training dives prior to observational dives to become familiar with the technique. Unfortunately, scientists often desire to abandon training dives when worthwhile observations are encountered during the training period.

7 SUMMARY

United States scientists have used scuba techniques during the past 12 years to effectively study the behavior of fish in their natural environment and to some extent within the influence of capturing gear.

Diving techniques at the Bureau of Commercial Fisheries Exploratory Fishing and Gear Research Base, Seattle, Washington, permit a close view of fish response to both midwater and bottom trawls. Divers descend to the operating trawl along the tow cable and move freely to all parts of the net.

Hand-held underwater cameras permit the underwater observer to document gear effectiveness and behavior patterns. Silt or organisms in the water occasionally restricts photographic success.

Several species of fish have been observed in and near trawls. Few fish appear alarmed by midwater trawls even after passing well into the large net. Herring and smelt behavior in a trawl has been observed for periods up to 20 min. Most flounders and other near-bottom species appear to react to a bottom trawl only when it is very close.

Some fish species respond to environmental conditions such as tide and food availability in such a way as to effect their availability to capture. Success with hook and line fishing was observed on one occasion to be dependent on precise positioning of the bait within the school.

Incidental observations by non-scientific divers has added to the total knowledge. While in British Honduras, divers photographed the response of anchovy schools to predators and to divers.

Water flow measurements in and around trawls have been taken by diver-held current meters. Herring were measured swimming in a trawl at over 2 kn for 20 min or more. Water flows measurably faster inside much of a midwater trawl than adjacent water on the outside. Back eddies in the cod end may permit a fish to rest and successfully renew escape attempts.

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STUDY OF SARDINE (Sardina pilchardus Walb.) BEHAVIOR IN THEIR NATURAL ENVIRONMENT BY ECHO SOUNDER AND ENVIRONMENTAL FACTORS

by

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Abstract

The author analyzes the behavior of sardines by means of the echo sounder in relation to environmental factors (light, feeding and temperature). In 1962 the sardine used to keep at the depth between 40 and 60 m (sometimes even deeper) by day, and migrated upwards (20 to 30 m) at dusk and at night. The schools were mostly compact by day and scattered at night, which was probably influenced by changes in the underwater illumination. Diurnal vertical migrations of sardine were greater when the thermocline in summer was less steep. It was observed during the fishing season that sardine migrated upwards through thermoclines of 0.6 to 2.5°C in about 5 to 10 m, but declined to move upwards or downwards through thermoclines of 4.5 to 6°C in about 2 to 5 m.

E/3

ETUDE AU SONDEUR A ULTRASONS DU COMPORTEMENT DE LA SARDINE (*Sardina pilchardus* Walb.) DANS SON MILIEU NATUREL PAR RAPPORT AUX FACTEURS AMBIANTS

Résumé

L'auteur a étudié à l'aide du sondeur à ultrasons le comportement de la sardine par rapport aux facteurs ambiants (éclairement, nourriture, température). En 1962, les poissons se tenaient de jour entre 40 et 60 m de profondeur (parfois même davantage), pour remonter (entre 20 et 30 m) au crépuscule et à la nuit. Les bancs étaient dans l'ensemble compacts le jour et dispersés la nuit, probablement sous l'effet de la modification de l'éclairement sous-marin. Les migrations verticales diurnes de la sardine étaient marquées lorsque la thermocline d'été était moins abrupte. On a observé durant la campagne de pêche que les sardines montaient en traversant des thermoclines où la température passait de 0,6 à 2,5°C en 5 à 10 m environ, mais ne se déplaçaient ni vers le haut ni vers le bas lorsque la thermocline accusait un "saut" de 4,5 à 6°C sur une distance d'approximativement 2 à 5 m.

ESTUDIO DEL COMPORTAMIENTO DE LA SARDINA (*Sardina pilchardus* Walb.) EN SU MEDIO AMBIENTE NATURAL MEDIANTE LA ECOSONDA Y FACTORES AMBIENTALES

Extracto

El autor analiza el comportamiento de las sardinas por medio de la ecosonda en relación con los factores ambientales (luz, alimentación y temperatura). En 1962 la sardina se mantenía generalmente de día a una profundidad comprendida entre 40 y 60 m (a veces incluso a una profundidad mayor), subiendo a aguas superiores (20 a 30 m) durante el crepúsculo y la noche. Los cardúmenes solían ser compactos durante el día y poco densos durante la noche, hecho en el que influían probablemente los cambios en la iluminación de las aguas inferiores. Las migraciones verticales diurnas de la sardina eran mayores en aquellas épocas del verano en que el gradiente de temperatura de la termoclina era menos acentuado. Durante la temporada de pesca se observó que la sardina emigraba a aguas superiores a través de termoclinas de 0,6 a 2,5°C en distancias verticales de unos 5 a 10 m, pero dejaba de moverse hacia arriba o hacia abajo a través de termoclinas de 4,5 a 6°C en unos 2 a 5 m.

1 INTRODUCTION

The study of the seasonal changes of water masses is of great importance to the knowledge of the biology of many sea organisms whose reaction to the changes in the hydrographic properties is either positive or negative. Such changes in the Adriatic occur mostly after cold and bitter winters. Pollak (1951) thinks that the regime of the Adriatic waters is under an intensive influence of meteorological factors as the Adriatic is a rather shallow sea. Due to its shallowness the Adriatic water structure follows the fluctuations of the existing "weather regime".

The admixture of the Adriatic waters is an important factor in increasing the productivity of the Adriatic water-masses. This phenomenon does not occur every year but it shows a more or less periodical rhythm of fluctuations (Županović and Zore-Armanda, 1963).

Županović (MS) has tried to correlate the more abundant catches of sardine taken in fishing seasons characterized by low temperatures with:

a) an intensive mixing of surface waters (upwelling) which produces favorable conditions for intensive feeding after spawning.

b) cooling of surface waters which stimulates schooling of adult sardine.

Furnestin (1953) has also underlined the importance of upwelling for the distribution of the Moroccan sardine (*Sardinella aurita*). Low temperature (15 to 18°C) in the summer period along the Moroccan coast enable this clupeid to live in the region while the temperatures of the open surface waters are above 20°C. Such upwelling movements correspond to the high productivity period which favors the development of plankton.

The results obtained from the investigations into the behavior of the sardine in the open middle Adriatic (Fig.1) would point out that in the areas where the thermocline was very well marked, the sardine kept above or under it. Under the thermocline it used to keep in the homothermal layer where temperature was about 15°C (Županović, 1965).

Kurc and Blancheteau (1966) have also attached great importance of the thermocline to the behavior of the sardine. By using artificial light they followed the reaction of the sardine in a relatively homogeneous water layer and in the layer where the thermocline was very well marked. In the cases in which the waters were relatively homogeneous from surface to bottom the schools of fish were found at all depths. On the other hand, where the thermocline was very well marked, the fish kept above or under it. Based on the results obtained, the authors think that the thermocline forms a very important thermal barrier which the fish generally do not cross, not even when instigated by such a strong stimulus as artificial light.

2 DIURNAL VERTICAL MIGRATION

2.1 Light

It is generally considered, that clupeids show "typical" diurnal migrations, i.e., towards the deeper layers by day, and nearer to the surface at night. The schools are usually compact by day and scattered at night. This behavior can be related to the light intensity. The use of echo sounders has enabled us to learn more about the movements and behavior of fish in their natural environment. Furnestin (1953) could follow on the echo-recording the "typical" diurnal cycle in the behavior of the Moroccan sardine. Cushing (1960) has related the depth of occurrence of pilchard (*Sardina pilchardus*) in the English Channel to the time of day. He found that fish schools were

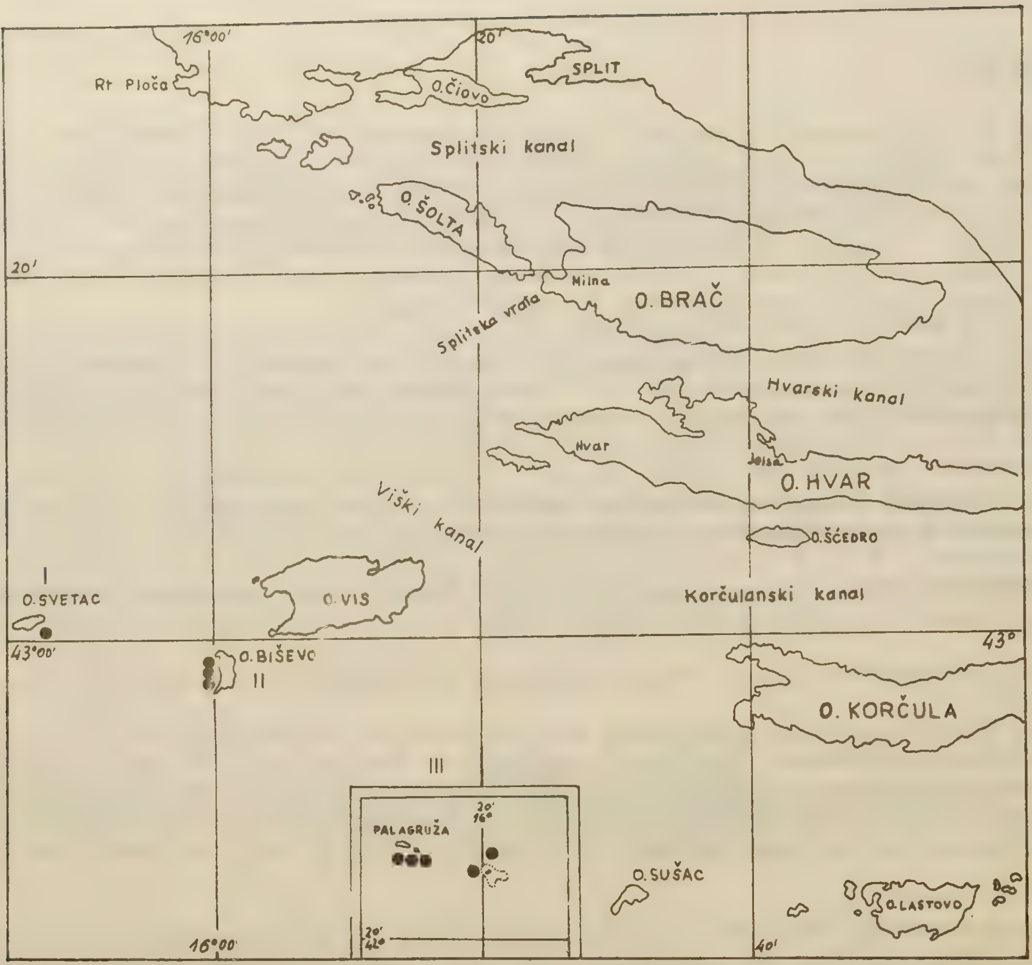
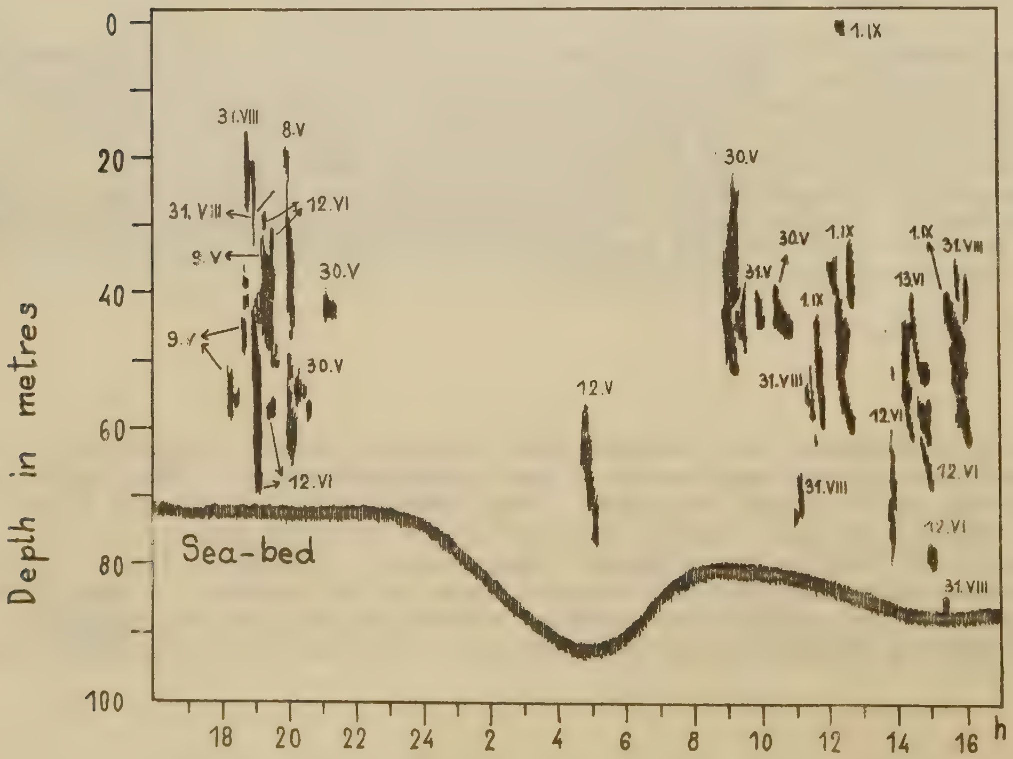

16°00'
20'
Rt Ploča
O.Čiovo
SPLIT
Splitski kanal
O. ŠOLTA
20'
Milna
O. BRAČ
Splitska vrata
Hvarski kanal
Hvar
Jelsa
O. HVAR
Viški kanal
O.ŠĆEDRO
I
O.SVETAC
O.VIS
Korčulanski kanal
43°00'
O.BIŠEVO
II
43°
O. KORČULA
III
PALAGRUŽA
20'
16°
O.SUŠAC
O.LASTOVO
20'
42°
16°00'
40'

Fig. 1 Fishing areas and localities of sardine catches



in deeper waters in the middle of the day, rising to 20 to 30 m at night. Richardson (1952) also observed that pilchard schools were deeper during daytime.

Dragesund (1964) has found, when investigating the sardine behavior in the Bay of Naples, that by day the fish aggregate in dense schools in deeper waters than at night. At dusk, the schools rise towards the surface and disperse. These reactions, according to the author's opinion, seem to correspond to the innate reactions of fish in relation to sunlight.

Also in our investigations into the diurnal behavior of sardine in the open middle Adriatic by means of the echo sounder we could ascertain that the fish schools are in deeper layers in the middle of the day, even at the very bottom, and at dusk and night they migrate upwards. In the middle of the day the sardine kept at the depth of 40 to 60 m (sometimes even deeper) and at dusk and night moved nearer to the surface (20 to 30 m). Figure 2 shows the vertical movements of sardine schools at different times of the day. The movements were followed from May to September, 1962.

The occurrence of sardine close to the surface in the middle of the day were observed by Belloc (1935); Furnestin (1953); and Cushing (1960). We do not know how much the above-mentioned behavior is associated with physiological factors.

2.2 Feeding

Vučetić (1963), analyzing the feeding of the adult sardine in the middle Adriatic, thinks that the diurnal vertical migrations of the sardine are probably associated with the changes of the light intensity and the diurnal vertical movements of plankton. The most intensive feeding of the sardine has been registered in the afternoon hours.

In winter months and at the beginning of spring the sardine keeps in deeper waters, and off the coast where it spawns (Gamulin, 1954; Gamulin and Karlovac, 1956; Karlovac, 1964). During this season we can find zooplankton organisms almost evenly distributed in all the layers from bottom to surface, even in day light. Such distribution of the zooplankton enables the sardine in the open middle Adriatic to feed intensively during the day in all the layers. In spring and at the beginning of summer when the zooplankton descends into the deeper layers (Hure, 1955, 1961) and its total quantity in the surface layer decreases, the sardine shows different behavior. This can probably be related to the zooplankton organisms, especially to copepods on which the sardine feeds. Vucetić (1961) found that temperature can influence the diurnal vertical migrations of copepods. Night migrations of Calanus helgolandicus in the southern Adriatic ceased in August (the month of maximum temperature) because of the thermocline. The thermal gradient was 0.14°C per 1 m. Voronina (1966) has found that in the Southern Ocean thermal gradients higher than 0.07°C per 1 m can influence the seasonal migrations of Rhincalcanus gigas, Calanus propincuus and Calanoides acutus.

2.3 Temperature

The appearance of fish on the surface, and their availability to fishing will depend considerably also upon a more or less expressed thermal gradient (thermocline). Schubert (1950) says that the northern North Sea herring does not migrate upwards through the thermocline of 6°C in 3 m, but it breaks through the thermocline of 2°C in 3 m. In more shallow waters it was found that the herring remains under the thermocline of 2°C in 5 m. Richardson (1952) has found that the herring passes through the thermocline of 2.45°C in 5 m. Biriykov (1958) has also found in the North Sea that the herring does not descend by day into deeper layers if the thermocline is too steep (from, e.g. 3° in about 10 m). It remains then at the deep of the thermocline, moving at night towards the surface.

The occurrence of the sardine in the upper layers in the middle Adriatic and its availability to fishing, will depend also upon the thermal gradient during the fishing season. This is indicated by preliminary results of our observations on the sardine

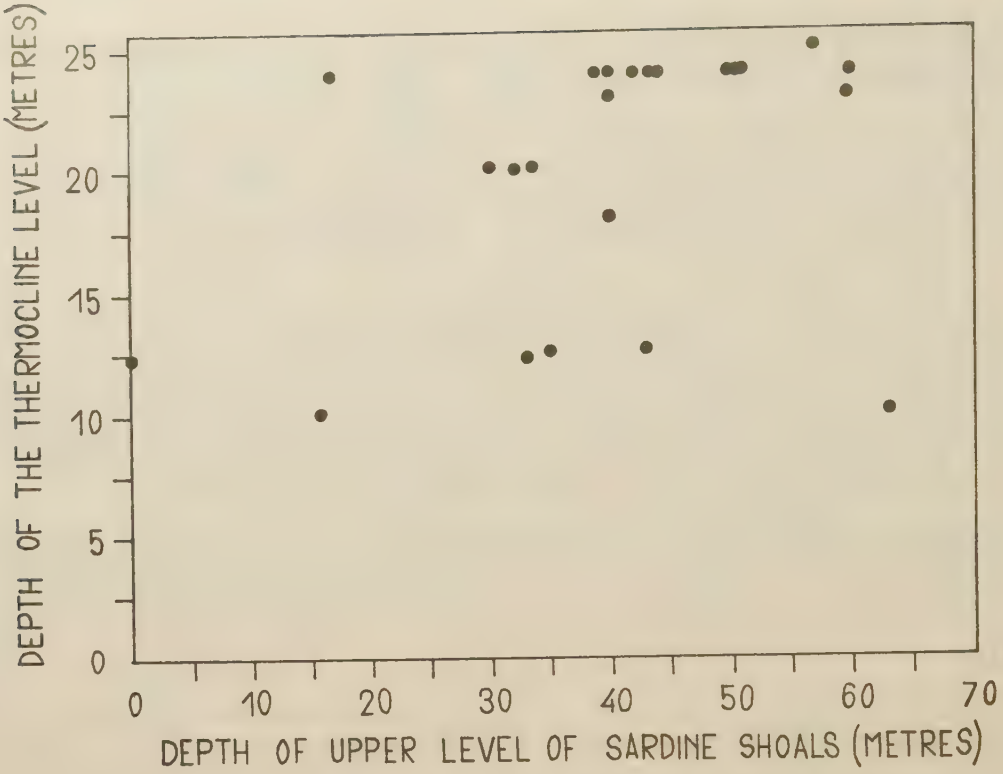


Fig. 3 The depth of sardine shoals at different levels

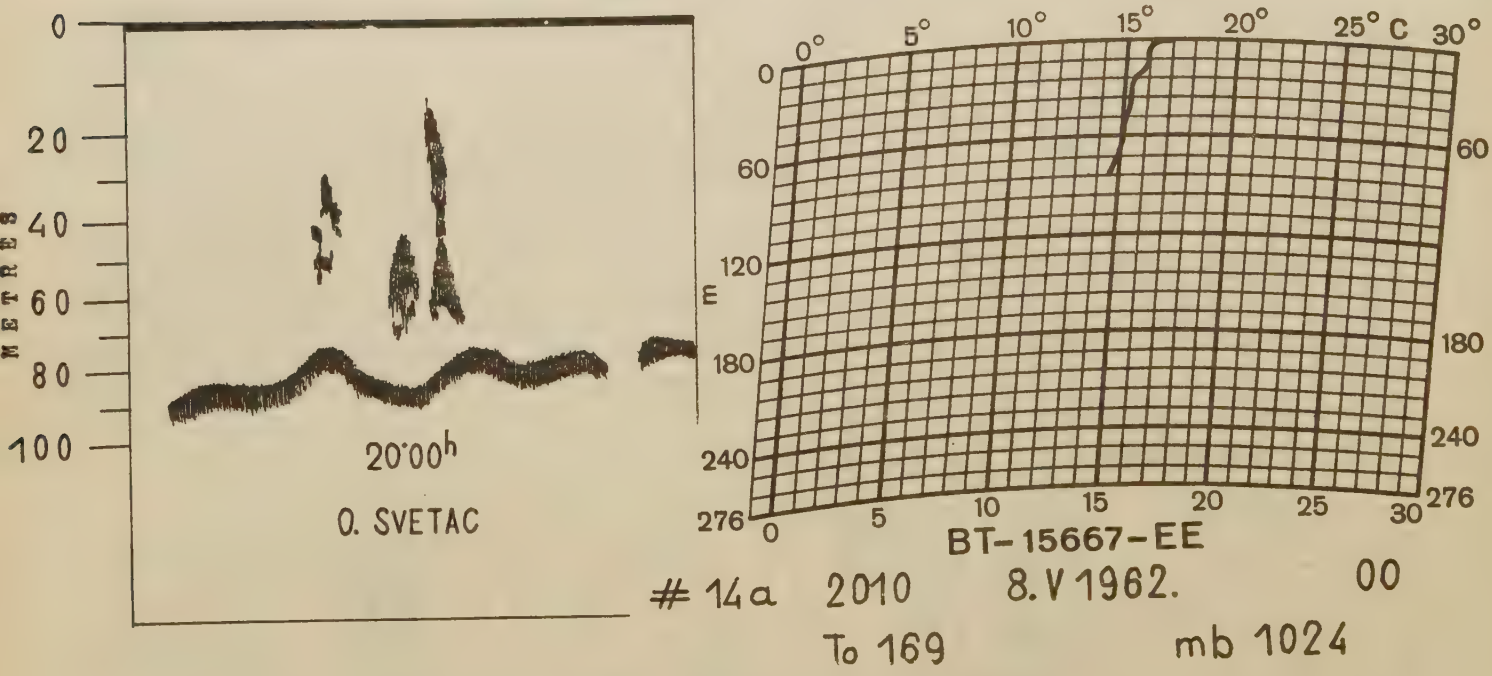


Fig. 4 Echo traces of sardine at dusk in the area of Svetac (I) Island, 8 May, and BT

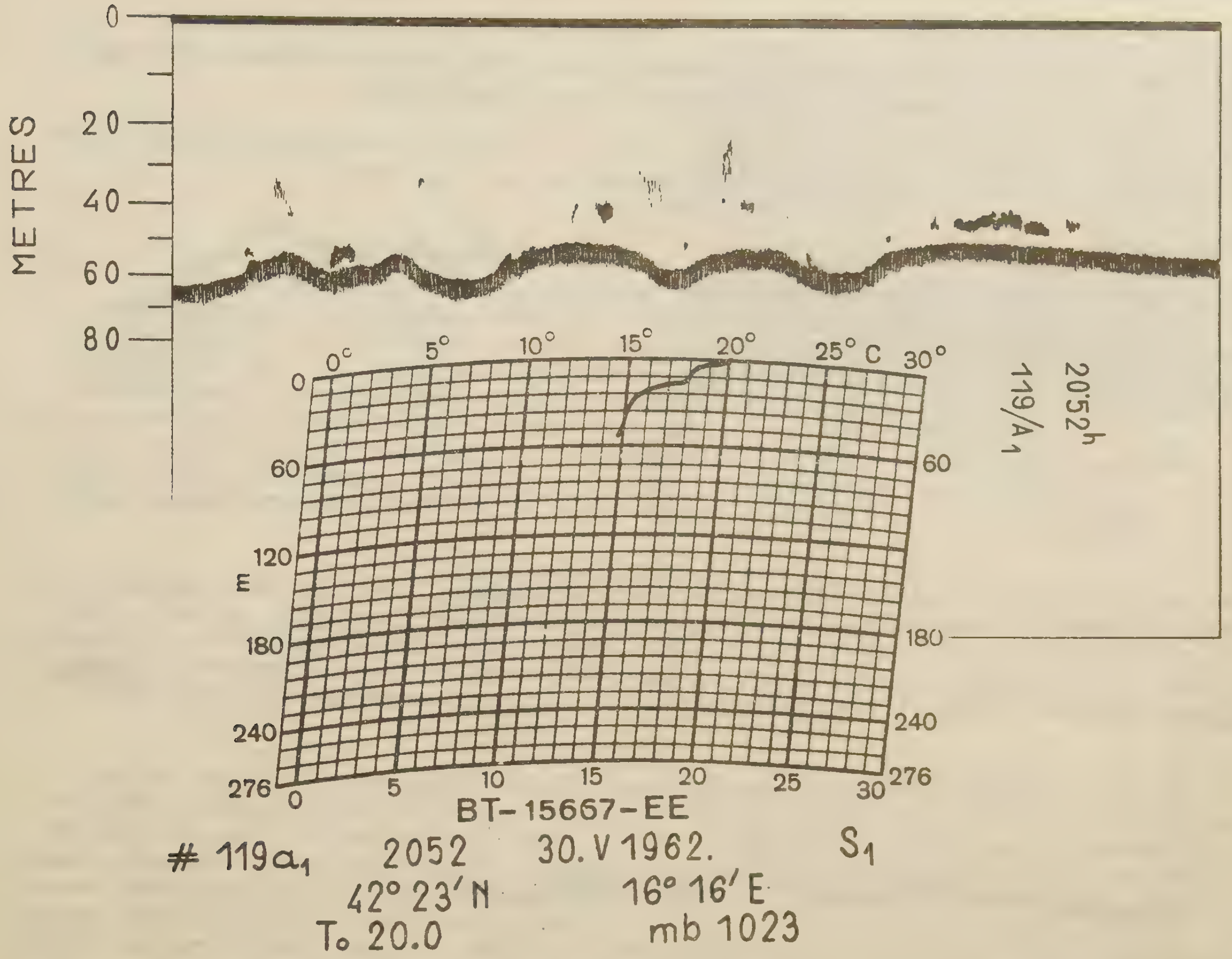


Fig. 5 Echo traces of sardine at dusk in the area of Palagruza (III) Island, 30 May, and BT

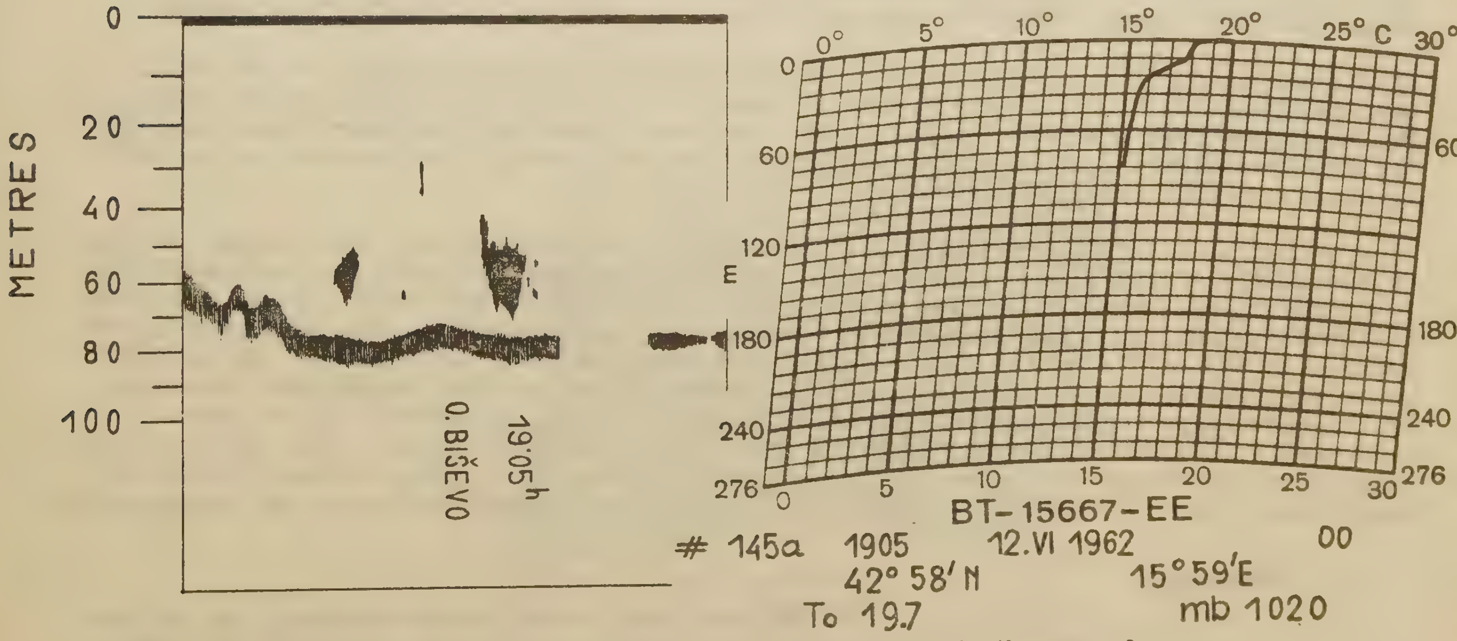


Fig. 6 Echo traces of sardine at sunset in the area of Bisevo (II) Island, 12 June, and BT

behavior in relation to temperature. Figure 3 shows the relation between the upper level of sardine schools and the depth levels of the thermocline.

The sardine mostly kept under the thermocline. It did not migrate upwards under the influence of artificial light if the thermocline was too steep.

2.4 Catch

The first catch of the sardine during a moonless night in the middle Adriatic in 1962 began on 7 May. On the Island of Svetac (I) that night 40 q of sardine were caught. The next day, i.e. 8 May, at 20.00 we found a large school of fish 500 m S off the Island of Svetac. The school was at the depth of 17–70 m. At the bottom it was more dense and compact and more dispersed towards the surface. The echogram (Fig.4) shows the finding of the fish on the echo-recorder. Concurrently, the sample of temperature was taken with a bathythermograph BT. The thermal gradient was 0.6°C in about 5 m. At the position where the school of fish was registered on the echo-recording the same night the fishermen caught 121 q of sardine with artificial light.

On the Island of Palagruza (III) on 30 May, at 20.52 h, the fish were registered at the very bottom. The echo traces of fish and the bathythermogram are shown on Fig.5. The thermal gradient was 2.5°C in about 8 m. The sardine broke through the thermocline at night. The fishermen caught 220 q of sardine and about 10 q of mackerel (Scomber Scombrus) the same night at the same positions. Fishing continued the next night.

On 12 June, the concentrations and behavior of the sardine were studied on the Island of Bisevo (II). At sunset, not far from the coast, a compact school of fish was registered at the depth between 40 to 70 m. The echo traces of fish and the BT are shown on Fig.6. The thermal gradient was 2°C in about 10 m. The fishermen caught that night, with artificial light, 90 q of sardine at the position to which they were sent. Not far from this position, at 17.25 h, fish traces were also registered on the echo sounder. The fish were at the depth between 30 to 50 m and kept under the thermocline. The echo traces of fish and the BT are shown on Fig.7. The thermal gradient was 2°C in about 8 m. The fishermen with artificial light were also sent to the place where fish were found. They caught about 100 q of sardine 16.1 to 18.7 cm length.

At the same position on 31 August, many fish traces were registered at the depth between 40 and 50 m. The echo traces of fish and the BT records are shown on Fig.8. The fishermen used artificial light at the positions where the fish were registered on the echo-recording. The fish did not migrate upwards through the thermocline of 4.5°C in about 5 m, but remained under it.

On the Island of Palagruza (III) a large school of sardine was found on the surface in the middle of the day on 1 September. At the same place BT data were obtained (Fig. 9). The thermal gradient in the surface layer was 6°C in about 2 m. It was believed that the sardine could not break through the steep thermocline but they remained on the surface in the middle of the day. It is characteristic that not far from the position where the sardine was seen on the surface, numerous smaller fish traces near the very bottom, (the shape of the traces pointing to sardine), were registered on the echo-recording. The echo traces of fish and the BT are shown on Fig.10. The water temperature near the bottom was about 15°C and it would correspond to the temperature of the homothermal layer of the water in which the sardine was registered under the thermocline.

2.5 Migration

Tagging results in the middle Adriatic have shown that, after spawning, and in the period of intensive feeding, sardines approach the continental shelf, (Mužinić, 1950, 1952). Such migrations were noticed in 1949 and 1950 (Županović, 1955), when the

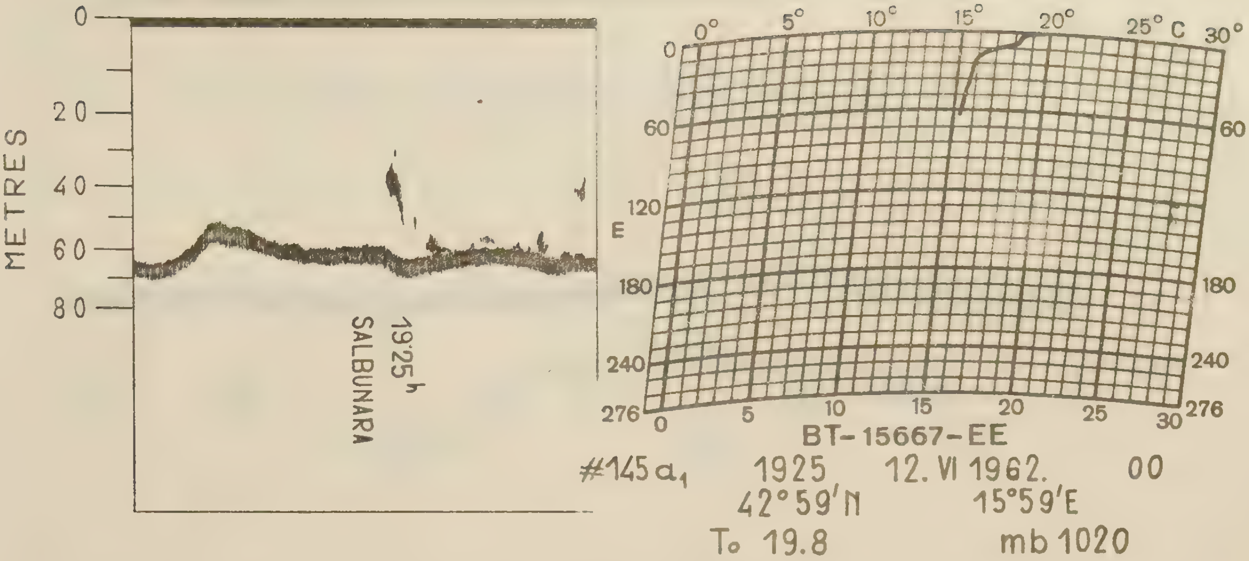


Fig. 7 Echo traces of sardine at sunset in the area of Bisevo (II) Island, 12 June, and BT

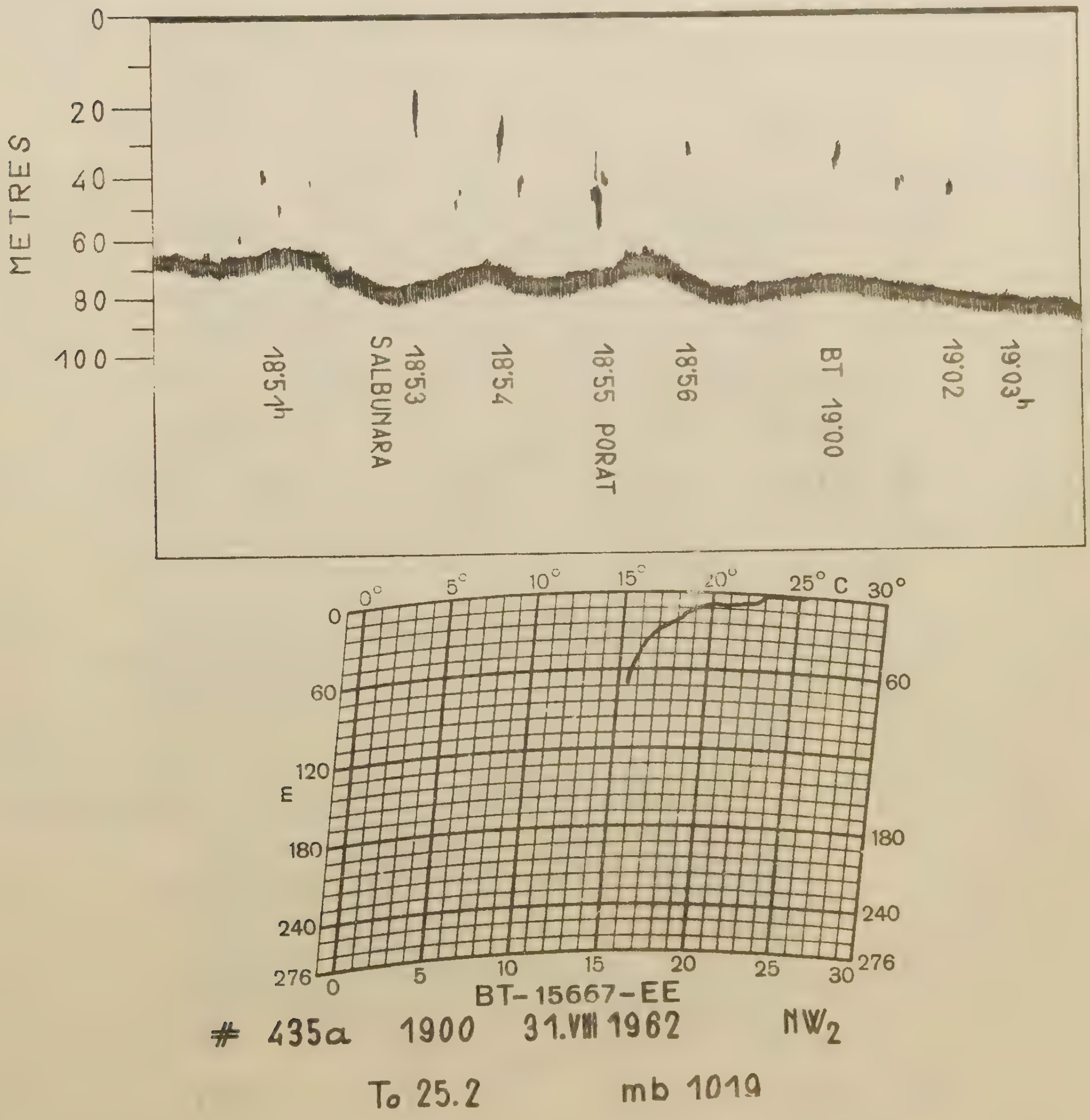


Fig. 8 Echo traces of sardine at sunset in the area of Bisevo (II) Island, 31 August, and BT

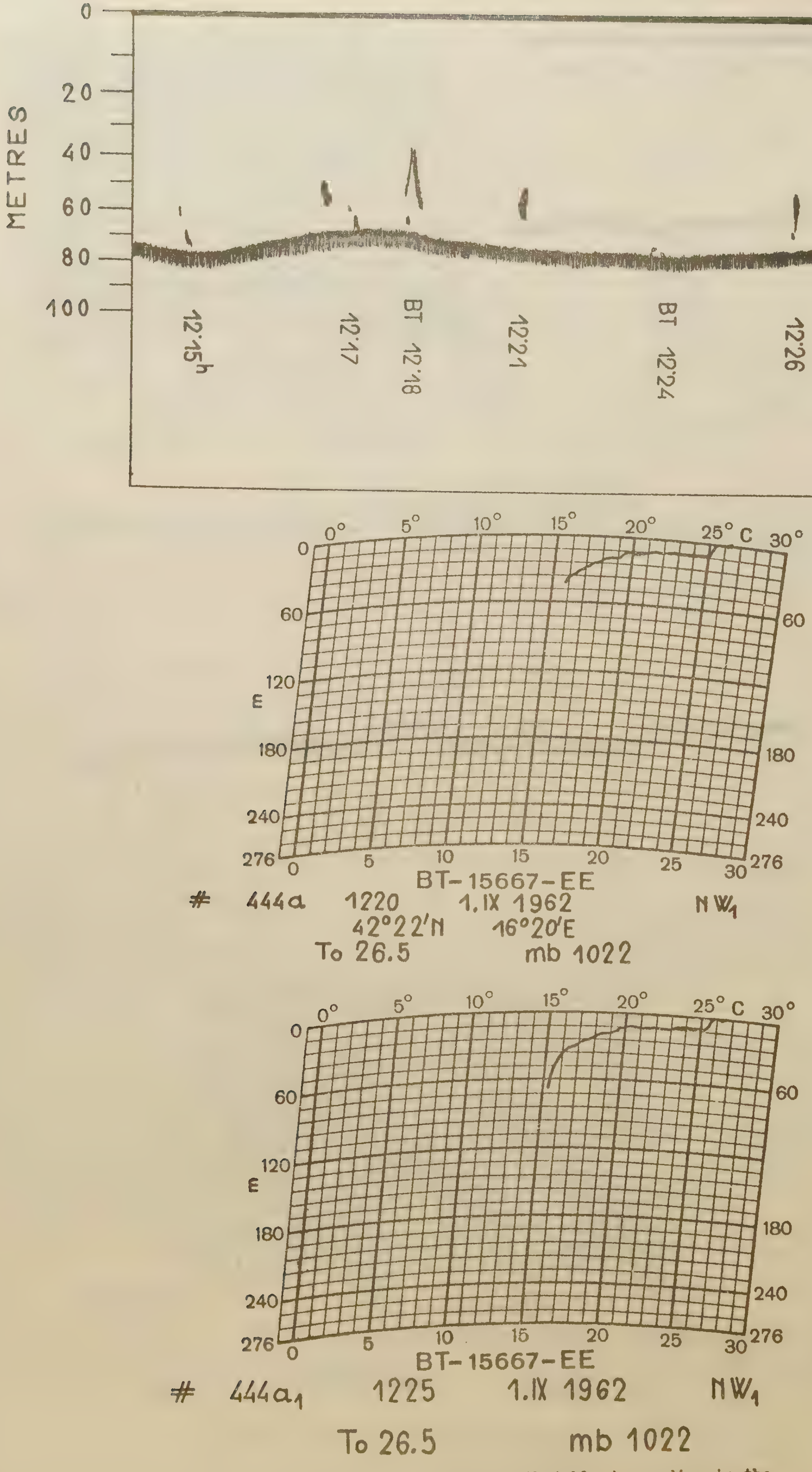


Fig. 9 Echo traces attributable to sardine in the middle of the day in the area of Palagruza (III) Island, 1 September, and BT

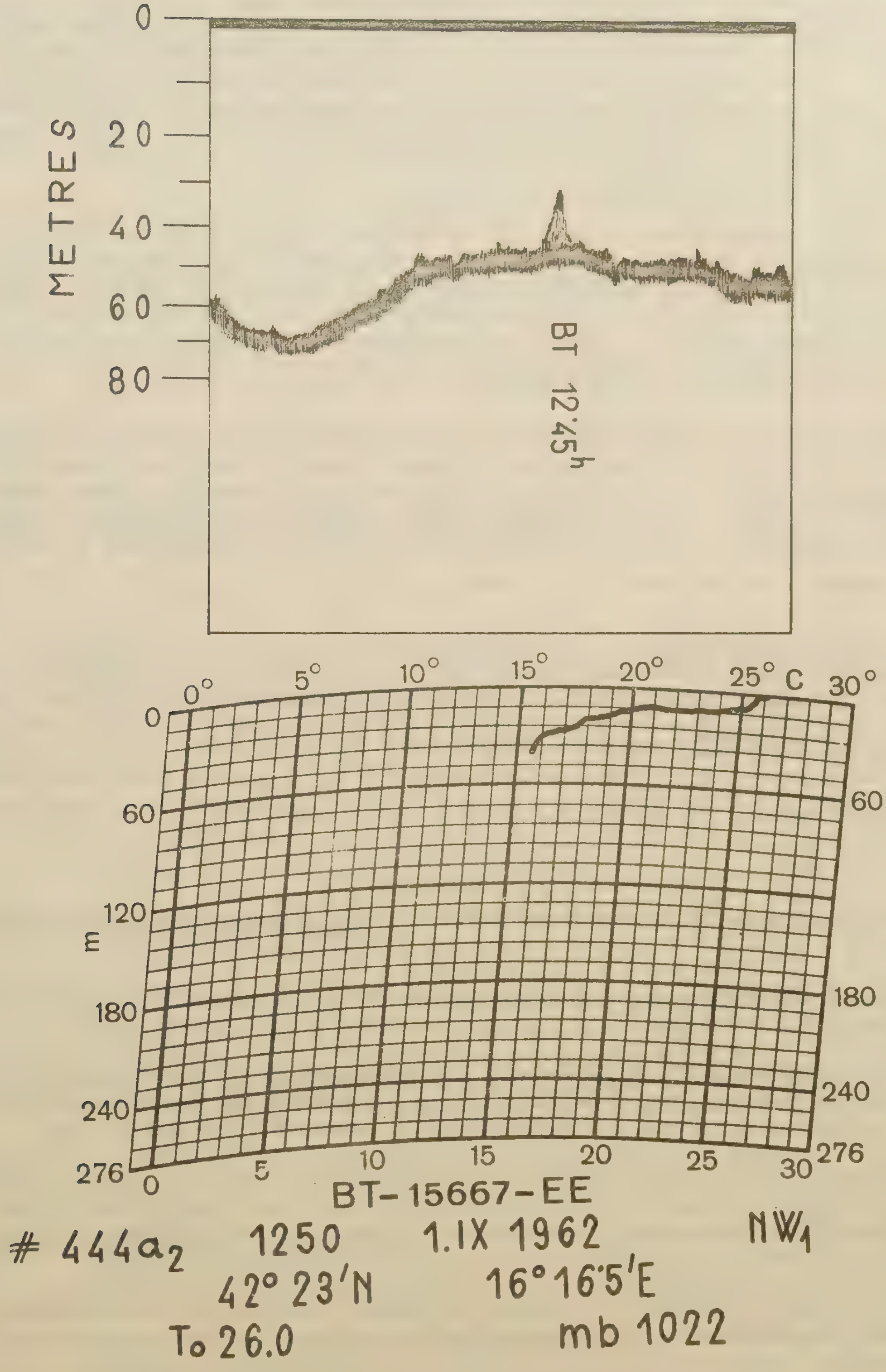


Fig. 10 Echo traces attributable to sardine in the middle of the day in the area of Palagruza (III) Island, 1 September, and BT

sardine moved from the open Adriatic towards the continental shelf. But the same phenomenon has not been observed in 1962, i.e. during our studies of sardine concentrations and distributions (Županović, 1964). The year 1962, contrary to 1949/1950, was poor in catches. The sardine catch along the shore and in the channel area was next to nothing. Some better catches were obtained in some distant fishing-grounds of the open middle Adriatic (Islands: Bisevo, Svetac and Palagruza). The phenomenon mentioned above shows that, in poor years, the sardine keeps to more open and distant waters.

The analysis of the temperature changes on the bathythermograms points out that the temperature gradient in the deeper water layers shows very small changes during the fishing season. Considerable differences were found only in the surface layers of water. Those changes could have influenced the availability and appearance of the adult sardine in the upper layers in 1962. Temperature conditions in these waters were exceptional. The temperature gradient in only some meters of depth under the very surface showed a difference of 7° to 8°C.

A comparison of temperature conditions in different water layers, and in different areas, allowed us to ascertain the preference of water layers of sardine, especially in the areas of the open Adriatic, where the sardine obviously remained after spawning, without approaching the coast. The fish usually kept deeper, i.e. under the thermocline, and in the neighbouring water layer, which showed mainly homogeneous properties.

3 CONCLUSION

A more or less intensive formation of the thermocline in the summer period can influence, not only the diurnal vertical migrations of the sardine in the middle Adriatic, but also its movement towards the coast after spawning, and during the period of intensive feeding. The diurnal vertical migrations were greater when the stability of the water masses in the summer period was smaller. In the fishing season the sardine broke through the thermocline of 0.6 to 2.5°C in about 5 to 10 m, but could not break through the thermocline of 4.5 to 6°C in the 2 to 5 m, so remained under or above it.

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L'APPLICATION A LA PECHE DES REACTIONS PHOTOTROPIQUES DES POISSONS

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Résumé

L'utilisation de lumière artificielle comme agent d'attraction représente un progrès sur les méthodes traditionelles de pêche au moyen d'appât. Cependant on connaît mal les motivations qui induisent les poissons à se diriger vers une source lumineuse et à y séjourner. Avant d'exposer les résultats des observations qu'il a faites sur le comportement du poisson, dans les conditions de la pêche en mer, l'auteur analyse les différentes théories qui tendent à rendre compte du "phototropisme" des poissons.

La connaissance des conduites de séjour des animaux dans un champ éclairé, qui dépendent de divers facteurs biologiques et abiotiques, permet de mettre au point un appareillage adéquat et d'améliorer une technique halieutique déjà ancienne.

Pour terminer, les perspectives d'avenir qu'offre l'utilisation conjointe de la lumière, d'une pompe à poisson et de l'énergie électrique, sont soulignées.

E/4

PHOTOTROPIC REACTIONS APPLIED TO FISHING

Abstract

The use of artificial light as an attractant is an improvement on traditional fishing methods using bait. However, little is known as to what induces fish to move toward a light source and stay there. An examination of the different theories attempting to explain phototropism in fish is followed by a discussion of the findings of observations on fish under conditions at sea.

An understanding of the behavior of animals in a light field, such behavior being governed by a number of biological and abiotic factors, suggests improvements of light-fishing gear and in these techniques which have been used since ancient times.

The outlook for the combined use of light, fish pumps and electric power are also discussed.

LA APLICACION A LA PESCA DE LAS REACCIONES FOTOTROPICAS DE LOS PECES

Extracto

La utilización de la luz artificial como agente de atracción constituye un progreso en relación con los métodos tradicionales de pesca por medio de cebo. No obstante, se conocen mal las motivaciones que inducen a los peces a dirigirse hacia una fuente luminosa y a permanecer junto a ella. Antes de exponer los resultados de las observaciones que ha hecho sobre el comportamiento de los peces, en condiciones de pesca en el mar, el autor analiza las diferentes teorías que tratan de explicar el "fototropismo" de los peces.

El conocimiento del comportamiento de los animales en un campo iluminado, que depende de diversos factores biológicos y abióticos, permite preparar todo el equipo necesario y mejorar una técnica de pesca ya antigua.

Por último, se ponen de relieve las perspectivas futuras que ofrece la utilización conjunta de la luz, de una bomba de succión y de la energía eléctrica.

1 INTRODUCTION

Les techniques halieutiques évoluent lentement, mais de façon constante. La conception des engins de pêche d'abord simples et passifs, comme les filets maillants, les nasses et autres pièges fixes, s'est peu à peu orientée vers des engins plus complexes mais surtout plus dynamiques comme, par exemple, divers types de sennes tournantes.

Dans le premier cas, on attend que le poisson, au hasard de ses déplacements, vienne se jeter dans le piège tendu; dans le second cas, au contraire, c'est l'homme qui, mettant à profit les mouvements des poissons, les contraint à se rassembler dans un cercle de filet qu'il resserre autour d'eux.

La connaissance empirique de certains aspects du comportement des poissons a permis de faire un pas de plus dans l'élaboration des méthodes de pêche. C'est ainsi que l'idée d'attirer le poisson par de la nourriture a, dans bien des cas, augmenté considérablement le pouvoir de capture d'un engin en faisant précéder d'une phase attractive la phase purement coërcitive qu'est l'encerclement par une paroi de filet du poisson ainsi groupé.

La production artificielle d'un tropisme alimentaire, en l'occurence un chimiotropisme dans un gradient de substances diluées, est un progrès certain. Toutefois, le prix de l'appât, généralement coûteux, doit être pris en considération. Pour qu'un appât soit valablement utilisé, il est nécessaire d'en employer de faibles quantités qui attireront beaucoup de poissons. Moins la capture sera élevée et plus cher sera cet appât. Or, moins le poisson est abondant et plus le pêcheur a tendance à jeter de l'appât à la mer dans l'espoir problématique d'accroître ses chances de faire de bonnes captures.

C'est ainsi que nous avons vu des pêcheurs du golfe de Gascogne vendre leurs sardines pour une somme inférieure à celle qu'ils avaient dépensée pour les attirer.

Il était donc important de remplacer la phase attractive alimentaire pour un autre agent d'attraction dont l'efficacité soit aussi bonne et dont le prix de revient soit inférieur. Or, l'un des plus anciennement connus est la lumière artificielle dont l'utilisation, tout au moins rudimentaire, doit remonter à la préhistoire. La pêche à la lumière, ou pêche au feu, est en effet, pratiquée depuis longtemps dans de nombreux pays et son rendement, quoique variable, est généralement excellent.

2 LES THÉORIES DU PHOTOTROPISME

Point n'est besoin de faire l'historique de la technologie de la pêche à la lumière. Elle n'a que peu évolué même si l'on utilise aujourd'hui des générateurs électriques qui peu à peu ont remplacé les appareils à gaz d'essence ou d'acétylène, voire les braises incandescentes et même les torches résineuses qui sont probablement à l'origine de cette méthode.

Cette technique a peu évolué avons-nous dit, parce qu'on emploie aujourd'hui des lampes électriques de la même manière empirique qu'on utilisait jadis un matériel rudimentaire. On sait, pour l'avoir constaté que la lumière attire les poissons, mais ce qu'on ignore, c'est pourquoi et comment le poisson est attiré.

Ce problème ne préoccupe d'ailleurs pas le pêcheur. Mais il appartient au biologiste et au technologiste des pêches de se pencher sur lui.

C'est ce qu'ont fait d'assez nombreux chercheurs qui ont étudié divers aspects à la fois techniques et psycho-physiologiques de la pêche au feu et qui ont tenté de bâtir des théories rendant compte du phototropisme des poissons. Ces théories, pour diversifiées qu'elles soient peuvent, en fait, se ramener à trois hypothèses principales.

1°/ Le poisson est attiré par la lumière parce qu'il répond à un phototropisme positif tout en recherchant une luminosité optimale. Il s'agirait d'un réflexe d'orientation et d'exploration pouvant varier selon la nature et l'intensité de la lumière émise et en fonction de divers facteurs abiotiques ou biologiques. Nombreux sont les auteurs qui se sont ralliés à cette théorie, et c'est aussi en partie notre cas.

Mais si le déterminisme des conduites phototropiques est certainment d'origine nerveuse, il n'est pas évident qu'il s'agisse toujours de réaction réflexe, car il nous est apparu que dans le cas de très jeunes individus, par exemple, il faut plutôt l'interprêter comme résultant d'une excitation directe.

Toutefois, pour les poissons adultes qui font l'objet de la pêche, c'est le plus souvent un réflexe qui se manifeste, c'est-à-dire une conduite motivée ressortissant à un niveau d'intégration centrale qui la distingue d'un "mouvement forcé", mais ne l'apparente pas pour autant à un réflexe conditionné qui supposerait un apprentissage incompatible avec les modalités de réponses, souvent bien plus rapides chez les formes juvéniles que chez les adultes.

2°/ Une autre hypothèse est celle qui explique l'attraction du poisson par une motivation alimentaire.

Si l'on recrée artificiellement les conditions qui lui permettent durant le jour de trouver des proies, il se comporte dans la zone éclairée, comme pendant sa vie diurne. Il ne s'agirait pas alors, d'un phototropisme, mais plutôt d'un transfert des habitudes écologiques.

Il est en effet indéniable que de nombreux poissons se nourrissent sous les lampes. Ainsi les sardines absorbent le plancton souvent très dense dans la zone d'éclairement tandis que des prédateurs comme les maquereaux et les chinchards pourchassent les sardines.

Peut-on avancer une interprétation intellectualiste qui expliquerait ce comportement par le fait que le poisson est capable d'établir une relation lumière artificielle-nourriture? Comment aurait-il pu "apprendre", sans être capturé, qu'une telle relation existe, et surtout, pourquoi les très jeunes individus encore "inexpérimentés", si l'on peut dire, répondent-ils plus rapidement à la lumière que les adultes?

Enfin comment peut-on expliquer que des prédateurs soient souvent attirés en grande quantité près des lumières et y séjournent longtemps, même en l'absence de proies?

Ces questions auxquelles il est difficile de répondre avec logique nous ont amené à rejeter une telle théorie. Nous avons en effet observé que si le poisson se nourrit lorsqu'il est attiré par la lumière, ce n'est pas parce qu'il veut se nourrir qu'il se dirige vers elle.

3°/ Une théorie originale qui est surtout le fait d'un chercheur hollandais, Verheijen, explique la prétendue attraction lumineuse par une désorientation photique du poisson qui se conduit de façon anormale lorsqu'il est placé dans des conditions anormales d'illumination. Son comportement serait comparable à ceux des insectes ou des oiseaux auxquels une source de lumière, dans la nuit, fait perdre le sens de l'orientation. Il ne s'agirait donc pas d'une phototaxie positive, mais d'une altération des mouvements et du comportement consécutive à l'excitation du système nerveux central qui serait commandé par les stimuli perçus par les organes optiques.

L'accroissement du nombre des poissons dans une zone artificiellement éclairée résulterait donc d'une augmentation statistique du nombre des individus désorientés et non d'un groupement dynamique. Cette théorie, en réalité bien plus élaborée que ce bref résumé ne le montre, ne peut cependant pas être appliquée d'une façon générale. Elle peut expliquer l'arrivée, près des lampes, d'un nombre restreint d'individus qui se comportent de façon désordonnée. Mais elle ne permet pas de saisir le processus d'attraction et de rétention, au voisinage des lampes, de bancs composés de plusieurs milliers de poissons.

En fait, il semble que seule l'approche des poissons vers les lampes ait retenu l'attention des observateurs. Les modalités du séjour dans le champ éclairé et sa durée n'ont guère fait l'objet d'études. Or, l'application du phototropisme à la pêche réside surtout dans les conduites des poissons qui vont s'établir de façon plus ou moins durable à une certaine distance des lampes.

Afin d'améliorer les techniques de la pêche à la lumière, ce sont ces comportements que nous nous sommes appliqués à définir chez quelques espèces pélagiques d'importance commerciale.

3 LES COMPORTEMENTS OBSERVÉS

Il convient tout d'abord de définir les termes que nous allons utiliser pour décrire les comportements des poissons.

Le tropisme, selon Viaud (1951) est un déplacement orienté qui ne cesse qu'au contact de la source émettrice du stimulus, et correspond à une recherche du maximum d'excitation; tel est le cas des insectes qui viennent se brûler à la flamme d'une bougie. Ce terme ne rend pas compte, comme nous le verrons, de la diversité des conduites des animaux attirés par nos lampes. Les taxies (Fraenkell et Gunn, 1940) ou pathies (Viaud), sont, elles aussi, des déplacements orientés, mais qui diffèrent des tropismes dans la mesure où l'animal excité par un stimulus, fuit un excès d'excitation et stabilise sa position par rapport à la source d'énergie en un point qui correspond à son préférendum.

Le processus d'approche étant ainsi défini comme une taxie, il nous reste à rendre compte des modalités de séjour des poissons dans un champ lumineux. Elles sont diverses selon les espèces et varient pour une espèce donnée en fonction de différents facteurs. Quoi qu'il en soit, elles peuvent se ramener à deux types principaux:

1°/ les conduites de cinèses qui sont des activations générales et non contrôlées de la motricité. Ces conduites qui correspondent à une recherche de l'excitation maximum semblent résulter d'une inhibition des centres supérieurs et doivent pouvoir, au moins dans certains cas, s'exprimer en terme d'excitation directe;

2°/ la conduite de photopréférendum qui, nous l'avons vu, fait suite à la taxie et correspond à une adaptation progressive à une situation donnée. A ce titre, ce comportement ressortit certainement à des niveaux d'intégrations nerveuses supérieures à celles des cinèses ou des simples tropismes.

Il est évident que si l'on se place dans les conditions normales de la pêche en mer, l'approche du poisson, sa taxie, échappe à l'observateur. Les comportements étudiés sont donc ceux des poissons déjà arrivés à proximité des lampes, mais il nous semble que pour l'application à la pêche, ce sont ceux-là qu'il importe surtout de bien connaître afin de pouvoir retenir les poissons, les concentrer en banc aussi compact que possible et adapter à leur comportement spécifique les manoeuvres de pêche.

Nous allons maintenant étudier les espèces importantes, principalement les clupéidés, qui ont fait l'objet de captures au cours de nos observations. Nous ne parlerons pas ici des espèces sans intérêt commercial, du plancton, des invertébrés, ni des poissons benthiques occasionnellement observés.

3.1. Sardines et sprats

Ces deux espèces ont, près des lampes, des comportements identiques. Seule leur taxie peut différer en fonction de facteurs abiotiques.

Lorsqu'ils ont atteint le champ lumineux, ces animaux ont, comme nous l'allons voir, des conduites qui varient suivant leur âge.

3.1.1. Conduites de cinèse Elles sont surtout le fait des formes juvéniles ne dépassent guère 5 cm de longueur. Ces jeunes apparaissent à l'observateur avant les adultes et nagent de façon déséquilibrée dans la zone d'éclairement maximum, ou même au-dessus des lampes immergées, exposant ainsi leur ventre à la lumière, ce qu'ils ne font jamais sous un éclairement normal.

Tantôt ils se déplacent très rapidement en ligne droite, dans une direction quelconque qui peut les amener hors du champ éclairé (orthocinèse), tantôt ils nagent en tous sens avec de brusques et fréquents changements de direction (clinocinèse). Cette activité incontrôlée correspond à une très forte dépense d'énergie qui fatique rapidement ces jeunes poissons dont bon nombre finit par être épuisé et se laisse emporter par le courant.

3.1.2. Adoption d'un photopréférendum Elle ne s'observe généralement que sur des sardines d'une taille au moins égale à 10 cm.

La taxie est plus lente chez elles que chez les jeunes poissons, mais leur conduite montre une adaptation progressive certaine à une situation artificiellement créée. Les poissons ne nagent presque jamais au-dessus des lampes. Suivant la clarté des eaux, ils se tiennent entre 1 et 5 m au-dessous d'elles et, la partie la plus abondante du banc attiré se tient à la limite du halo lumineux.

Lorsque les animaux sont ainsi groupés, ils nagent de façon tranquille, avec de rares et courts intermèdes cinétiques pour ceux d'entre eux qui s'approchent parfois des lampes durant l'activité alimentaire qu'ils manifestent souvent au détriment du plancton photophile. Il nous paraît évident que cette activité découle d'une bonne adaptation aux conditions lumineuses: les sardines, se trouvant après un laps de temps dans une situation qui ne provoque pas d'inhibition peuvent accessoirement s'alimenter. Mais il faut bien se garder de croire que c'est pour s'alimenter qu'elles viennent sous les lampes.

Ce comportement résultant d'une bonne adaptation sensorielle trouve une application pratique très importante dans la mise en oeuvre de la pêche au feu car les poissons à conduite de préférendum séjournent généralement en dehors du champ d'éclairement maximum.

Techniquement, on sait que chaque fois que la senne tournante est calée à l'intérieur du champ éclairé, les captures seront dérisoires, voire nulles, même si l'on a observé de grandes quantités de poissons. En revanche, le filet jeté en dehors du halo ramènera généralement de bonnes prises.

Une autre application du préférendum peut être trouvée dans la réduction du rayon du champ d'éclairement par diminution de l'intensité lumineuse. On constate alors que la lumière étant diffusée de moins en moins loin de sa source, le poisson s'en approche de façon à rester dans la zone d'éclairement optimale qu'il a choisie. Il est alors possible de le regrouper et de le capturer même avec de courtes sennes.

3.2. Anchois

3.2.1. Conduites de cinèses Ces conduites s'observent chez les jeunes anchois comme chez les autres clupéidés. Mais ils paraissent mieux s'adapter à un stimulus relativement violent si bien qu'ils montrent, à la longue, une tendance à l'adoption d'un préférendum. Les jeunes anchois attirés très rapidement à la lumière, nagent d'abord de façon très heurtée (clinocinèse), puis plus tranquillement et moins près des lampes, avec cependant de brefs retours à une conduite cinétique. Ces poissons peuvent donc, à l'inverse des jeunes sprats et sardines, séjourner longtemps, parfois durant plusieurs heures, près des lampes.

Les thoniers qui ont besoin d'appât vivant pour la pêche des germons et des thons rouges peuvent ainsi aisément capturer des anchois au feu et les conserver dans des viviers où ils s'accoutument rapidement à nager autour d'une lampe (40 W) immergée.

3.2.2. Adoption d'un photopréférendum Elle est le fait des individus de grande taille âgés de deux ans et plus.

Leur taxie est nettement moins rapide que celle des jeunes. En revanche, ils ne présentent jamais de cinèses. Ces observations qui corroborent pour l'Atlantique celles d'autres chercheurs en Méditerranée (Bini, 1961; Dragesund, 1964), nous ont amené à mettre au point une technique d'attraction appliquée à la pêche de cette espèce. Elle consiste essentiellement à utiliser des lampes immergées (Fig. 1) d'une puissance de 2000 W (4 lampes de 500 W) sous une tension constante de 24 v.

Des lampes maintenues hors de l'eau ont donné des résultats nettement moins bons.

Quant à la variation et à la diminution d'intensité, pratiquées avec succès pour la pêche des sardines, elles n'ont donné que des résultats négatifs, les anchois se dispersant au lieu de se concentrer vers leur zone de préférendum. Ceci doit pouvoir être expliqué par le fait que les anchois manifestant un phototropisme très rapide en présence d'un stimulus lumineux violent, l'"effet de piège" des lampes est dû, pour une part, à des réponses clinocinétiques préalables à la recherche d'un préférendum photique.

Quoi qu'il en soit, la connaissance des conduites de ces clupéidés au voisinage des lampes a permis pour chacun d'eux de mettre au point et d'améliorer les techniques de pêche.

4 FACTEURS INFLUANT SUR LES COMPORTEMENTS

Nous avons vu que les comportements varient par espèce en fonction de l'âge et donc de facteurs physiologiques.

D'autres facteurs, abiotiques, ont également une influence non négligeable sur ces comportements et surtout sur les modalités d'approche et de séjour des poissons près des lampes. Ce sont ces facteurs qui, en définitive, permettent ou non de capturer le poisson.

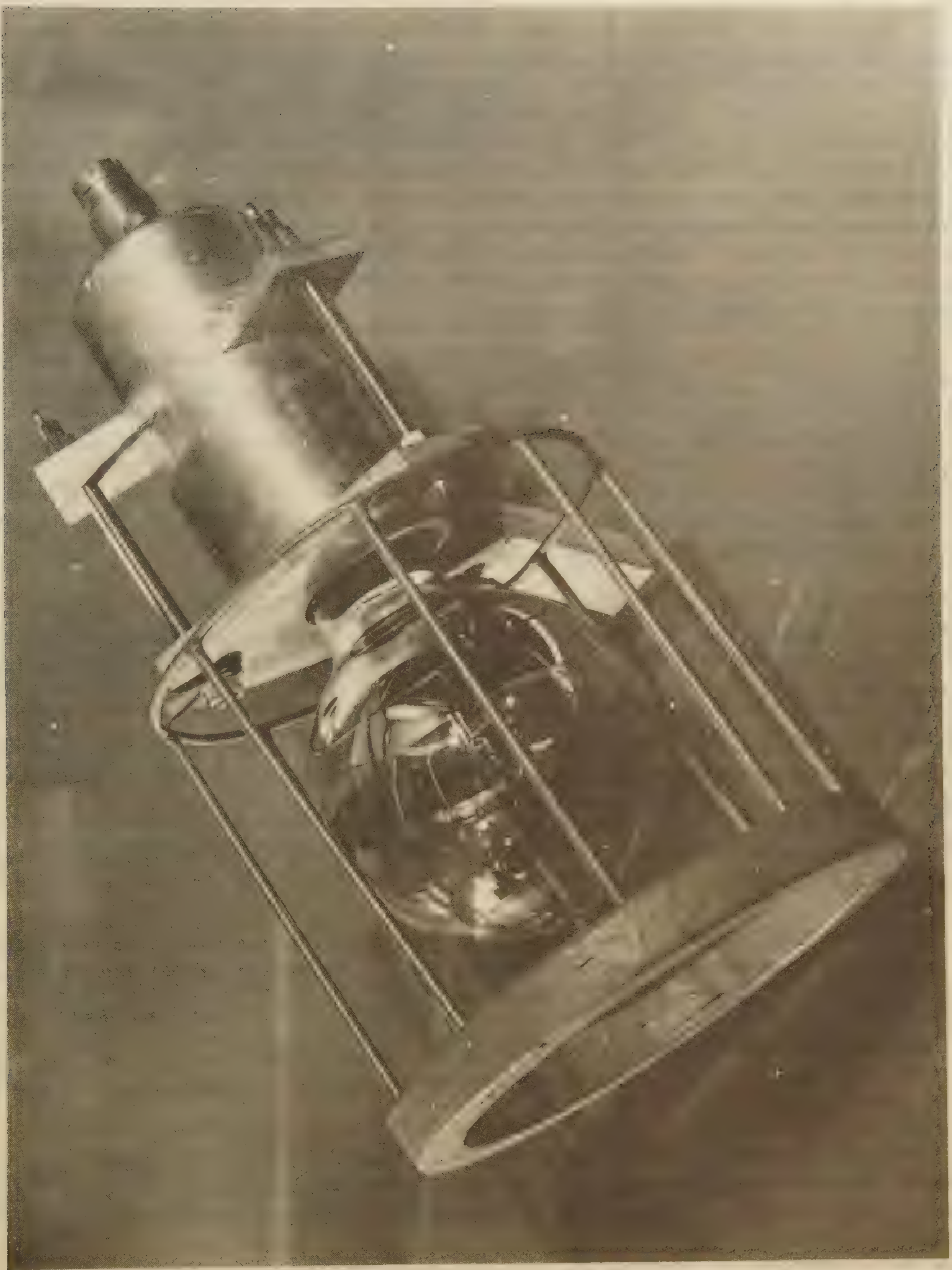

Fig. 1 Lampe de 500 W avec douille pouvant être immergée jusqu'à 50 m, mise au point par l'Institut scientifique et technique des Pêches maritimes (Photo: Laudren à Lorient)

Il nous faut tout d'abord insister sur les variables hydrologiques. Pour la plupart des clupéidés, l'un des paramètres ayant la plus grande influence sur leurs concentrations et leurs migrations est la température de l'eau. Par exemple, on trouve des sardines, qui sont relativement eurythermes, dans des eaux de températures extrêmes comprises entre 13 et 20°. Mais les températures optimales pour elles sont de l'ordre de 16 à 18° : lorsque ces températures favorables se retrouvent de la surface au fond, des sardines seront attirées par les lampes de pêche et l'écho-sondeur nous montre qu'elles sont relativement peu groupées et qu'elles se tiennent entre le fond et la proximité des lampes. Des observations faites en plongée sous-marine ont montré que les plus petits individus sont massés près de la surface et que les plus éloignés des lampes sont les poissons les plus grands.

Mais s'il existe une thermocline à fort gradient, deux cas peuvent se présenter qui sont illustrés par des données précises relevées en mer au cours de nos recherches:

1°/ températures variant de 17°9 en surface à 11°8 à 30 m avec une thermocline à 14°1 à 15 m.

Des sardines se trouvant dans la couche superficielle ont été rapidement groupées par la lumière et n'ont pas dépassé la profondeur de 15 m;

2°/ des sprats étant détectés entre 30 et 40 m de profondeur dans des eaux à 12°5 se sont élevés jusqu'à 25 m et n'ont pas pu être attirés près de la surface. Or, la thermocline se situait entre 20 et 30 m où la température de l'eau s'abaissait brutalement de 16°4 à 12°5.

Ces exemples nous montrent l'importance des facteurs hydrologiques qui peuvent expliquer partiellement pourquoi des poissons à phototropisme positif ne sont pas toujours attirés par des lampes de pêche.

D'autres agents interviennent aussi pour favoriser ou gêner le phénomène d'attraction photique.

L'un des plus importants semble être la lune dont les variations de phase incitent les pêcheurs à prendre la mer ou à rester au port. On sait en effet que la période de pleine lune est défavorable à la pêche au feu.

Nos essais ont montré que l'efficacité des lampes maintenues hors de l'eau diminuait avec l'augmentation de clarté lunaire, le moment le plus défavorable étant celui de la pleine lune.

En revanche, des essais de pêche poursuivis pendant toutes les phases de la lunaison avec des lampes immergées, nous ont amené à conclure qu'il n'y a pas, dans ce cas, de corrélation directe entre la phototaxie et l'illumination des eaux due à la lune.

Il est d'ailleurs évident que la lumière émise par une lampe hors de l'eau est réfléchie, pour sa majeure partie, par la surface et qu'elle est aisément concurrencée dans ce cas par la lune. Les poissons ne seront donc pas nécessairement induits à se grouper près des lampes dont la luminosité apparente n'est pas sensiblement supérieure à l'éclairement ambiant. Au contraire, la lumière d'une lampe immergée est suffisamment bien diffusée dans l'eau pour provoquer une phototaxie chez les poissons, même en période de pleine lune.

Il nous reste à déterminer l'influence de la nature et de la puissance de la lumière émise par les lampes de pêche.

En dépit de diverses recherches faites sur le pouvoir attractif de différentes couleurs de lumière, la plupart des professionnels utilisent la lumière blanche de lampes à incandescence. C'est également ce que nous avons fait. Pourtant, on sait que l'atténuation dans l'eau de la lumière blanche, qui renferme la totalité du spectre visible, est importante. Les seules parties du spectre qui soient bien diffusées sont celles qui correspondent au bleu-vert avec une longueur d'onde de 4 600 à 4 800 Å. Certains travaux ont déjà démontré que cette couleur semble permettre de bons rendements de pêche, en particulier sur les clupéidés. Cette question doit cependant faire l'objet d'études complémentaires que nous nous proposons d'entreprendre.

Mais d'ores et déjà nous avons déterminé empiriquement l'appareillage susceptible de permettre de bonnes pêches. Il consiste en un générateur diesel de 10 CV couplé à un alternateur pouvant fournir une puissance de 5 Kw sous une tension de 24 V. Il suffit généralement d'utiliser 4 lampes immergées de 500 W pour obtenir de bons resultats. Cette technique pourrait vraisemblablement être améliorée par l'utilisation de lampes à gaz ou à vapeur dont le spectre plus étroit et mieux diffusé dans l'eau permettrait de réaliser une économie d'énergie.

Des recherches dans ce sens seront poursuivies par l'Institut scientifique et technique des Pêches maritimes, corrélativement avec des observations sur le comportement des poissons et avec des études sur la physiologie de la vision.

5 PERSPECTIVE D'AVENIR

Un progrès a été accompli grâce à une connaissance, encore imparfaite, des conduites des poissons et par l'application à la pêche de leurs réponses à un stimulus photique produit plus économiquement qu'un tropisme alimentaire déterminé par un coûteux appât.

Un progrès plus décisif encore pourrait être accompli si l'on pouvait remplacer la senne, d'un maniement relativement difficile, par un autre engin plus aisément manoeuvré et ayant un pouvoir de capture plus élevé. La méthode apparemment la plus simple consisterait à pomper directement le poisson dans l'eau.

Mais on a vu que les concentrations les plus importantes de poissons attirés par la lumière résultent de l'adoption d'un préférendum photique qui peut se situer à plusieurs mètres des lampes. Il est donc nécessaire d'amener les animaux à franchir la distance qui sépare l'embouchure de la pompe de leur lieu de séjour. Un stimulus électrique, déjà utilisé dans certains cas en U.R.S.S., devrait pouvoir combler ce hiatus.

En effet, les recherches poursuivies dans différents pays nous amènent à penser que "la taxie anodique" en courant rupté est l'intermédiaire souhaitable entre l'approche délibérée, maïs limitée causée par la lumière et la succion mécanique exercée par la pompe; elle constitue un "mouvement forcé" qui se situe à mi-chemin de l'attraction et de la "coërcition" (Blancheteau et Kurc, 1966).

Bien entendu, de nombreux problèmes difficiles restent à résoudre pour que l'on puisse utiliser simultanément l'attraction photique, assez bien connue et l'attraction électrique dont certains effets physiologiques le sont également, mais dont l'adaptation sur le plan physique implique encore de longues recherches.

6 CONCLUSION

Nos recherches sur les problèmes de la pêche au feu ont été faites dans un but essentiellement technique. Nous désirions démontrer aux pêcheurs français de l'Atlantique qu'en utilisant des lumières artificielles, ils pourraient réaliser des meilleures captures qu'au moyen de l'appât traditionnel, fort coûteux, constitué d'oeufs de morue salée (rogue).

Mais il faut aussi souligner l'apport pratique d'une étude théorique. La distinction entre les notions de "cinèse" et de "préférendum" fondée sur l'observations directe effectuée dans les conditions de la pêche a permis de préciser certains caractères de l'intensité et de la durée d'éclairement ainsi que les limites du champ lumineux utilisable. C'est ainsi que grâce à des observations sur le comportement des poissons pélagiques, la pêche au feu, pourtant fort ancienne, a pu être modernisée et mieux adaptée à la capture des différentes espèces.

Enfin, l'utilisation de la lumière, qui est un excellent agent d'attraction, devrait permettre de transformer certaines techniques halieutiques en constituant le relai indispensable à la pêche électrique.

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UN CHALUT CONÇU EN FONCTION DU COMPORTEMENT DES CREVETTES

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Résumé

Un chalut à crevettes d'un type nouveau a été conçu par un pêcheur français, M. Pierre Devismes. Des observations sur le comportement de ces crustacés, faites en eau de mer, en traînant un modèle réduit de chalut, ont permis de constater que les crevettes soulevées par le bourrelet du chalut nagent par bonds successifs vers la partie supérieure de l'engin. Une nappe intermédiaire dite "sélective" a donc été placée dans le chalut de façon à le partager longitudinalement en deux parties terminées chacune par une poche. Les crevettes traversent cette nappe et sont recueillies dans la poche supérieure tandis que les invertébrés benthiques et les poissons se dirigent vers une poche inférieure d'où une partie d'entre eux peuvent s'échapper à travers les mailles de grande dimension.

E/5

TRAWL DESIGN BASED ON SHRIMP BEHAVIOR

Abstract

A novel shrimp-trawl has been designed by a French fisherman, Mr. Pierre Devismes. Observations on shrimp behavior conducted in seawater, by towing a scale-model trawl, revealed that shrimps lifted up by the groundrope swim toward the upper part of the trawl in several "jumps". A panel of "selective" webbing is placed in an intermediate position within the trawl in such a way as to divide the net into two (upper and lower) sections, each terminating in a bag. The shrimp pass through the panel and collect in the upper bag, while bottom invertebrates and fish are diverted into the lower bag, where some of them may escape through the larger meshes there.

UNA RED CONCEBIDA EN FUNCION DEL COMPORTAMIENTO DE LOS CAMARONES

Extracto

El pescador francés M. Pierre Devismes ha inventado una red de un nuevo tipo para pescar camarones. Observaciones sobre el comportamiento de estos crustáceos, hechas en agua de mar, arrastrando un pequeño modelo de red, han permitido comprobar que los camarones puestos en movimiento por la relinga de la red, nadan en saltos sucesivos hacia la parte superior del arte. En la red se ha colocado un paño intermedio llamado "selectivo", con objeto de dividirla longitudinalmente en dos partes, cada una de las cuales termina en un saco. Los camarones atraviesan este paño, yendo a parar al saco superior, mientras que los invertebrados bénticos y los peces se dirigen hacia un saco inferior del cual puede escapar una parte de ellos a través de las mallas grandes.

1 INTRODUCTION

La plupart des nations tendent vers l'intensification de leur effort de pêche pour faire face à la demande, sans cesse accrue, de produits de la mer. Simultanément, les océanographes des pêches cherchent à protéger les espèces dont beaucoup sont surexploitées. Ces deux points de vue sont apparemment inconciliables. Cependant, l'expérience a montré que dans certains cas, une bonne connaissance du comportement des espèces marines peut permettre la mise au point d'engins de pêche qui soient à la fois sélectifs et de bon rendement.

2 COMPORTEMENT ET PECHE DES CREVETTES

C'est ainsi que pour la pêche des crevettes grises (Crangon crangon L.) un type nouveau de chalut permet depuis peu de capturer les crevettes tout en sauvegardant l'essentiel des poissons.

Cet engin est dû à l'ingéniosité d'un pêcheur français, M. Pierre Devismes, qui a observé le comportement des crevettes se trouvant brusquement placées devant un chalut en réduction tiré au long d'une plage. Il a remarqué que les crevettes dérangées par le bourrelet du chalut nageaient très rapidement par bonds successifs les éloignant du sol selon une trajectoire oblique. Ce comportement l'a incité à confectionner un engin original comprenant une nappe intermédiaire aboutée au dos du chalut et cousue aux ralingues de côtés. Cette nappe est légèrement tirée vers le ventre du chalut par des tresses plombées. Elle divise ainsi l'intérieur du filet en deux parties superposées qui se terminent vers l'arrière par deux orifices auxquels deux poches distinctes viennent se raccorder.

La nappe intermédiaire aux mailles de 25 mm de côté laissera aisément passer les crevettes vers la poche supérieure qui les retiendra (mailles de 12 mm) tandis que les poissons qui ne pourront pas la traverser se trouveront, de ce fait, dirigée vers la poche inférieure, faite d'un maillage suffisamment grand pour ne retenir que les animaux de taille marchande (Fig. 1 et 2). La faune et la flore benthiques qui habituellement encombrent le chalut et détériorent une partie des crevettes, se trouvent également rejetées vers la poche inférieure que l'on peut même laisser ouverte, par exemple, lorsque les méduses sont trop abondantes. Dans ce dernier cas, l'expérience a montré que les captures de crevettes restent normales.

A la suite d'une démonstration faite en baie de Somme, en janvier 1964, par l'inventeur du chalut sélectif, nous avons repris l'expérimentation de cet engin et étudié les possibilités d'adaptation du dispositif de sélectivité sur des chaluts classiques.

Des observations ont ainsi été faites à différentes saisons, sur les principaux secteurs de pêche français de la Manche et du golfe de Gascogne.

Pour les besoins de l'expérience, les poches inférieure et supérieure, ont été confectionnées avec le même maillage (12 mm). De cette façon, il était possible de connaître avec précision les quantités de crevettes ayant ou n'ayant pas traversé la nappe intermédiaire.

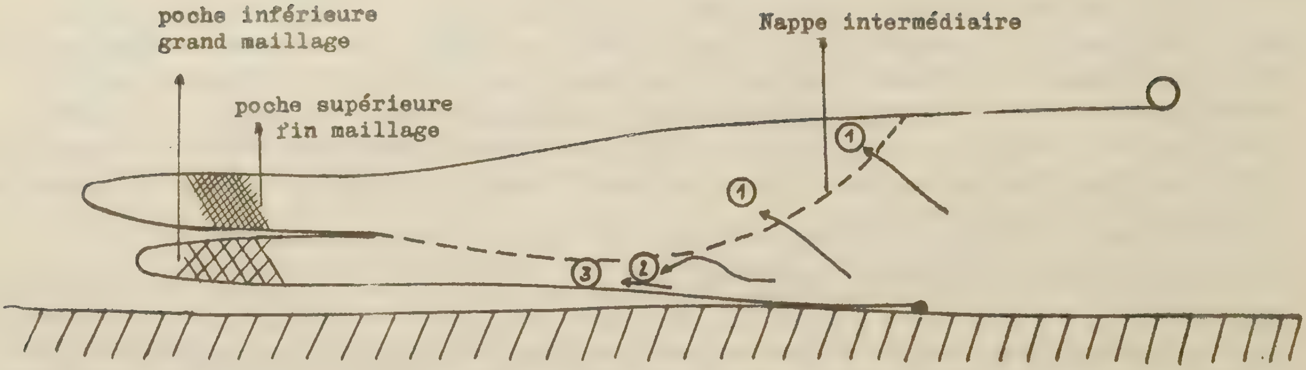
poche inférieure
grand maillage
poche supérieure
fin maillage
Nappe intermédiaire
①
①
②
③

Fig. 1 Coupe schématique d'un chalut sélectif à crevettes de type Devismes

(1) Les crevettes nagent à une certaine distance du fond et passent à travers la nappe intermédiaire

(2) Les poissons plats sont rejetés vers la poche inférieure par la nappe intermédiaire, ou

(3) nagent près du fond en direction de la poche inférieure. Tous les autres organismes benthiques sont également dirigés vers cette poche

(d'après ISTPM Boulogne)

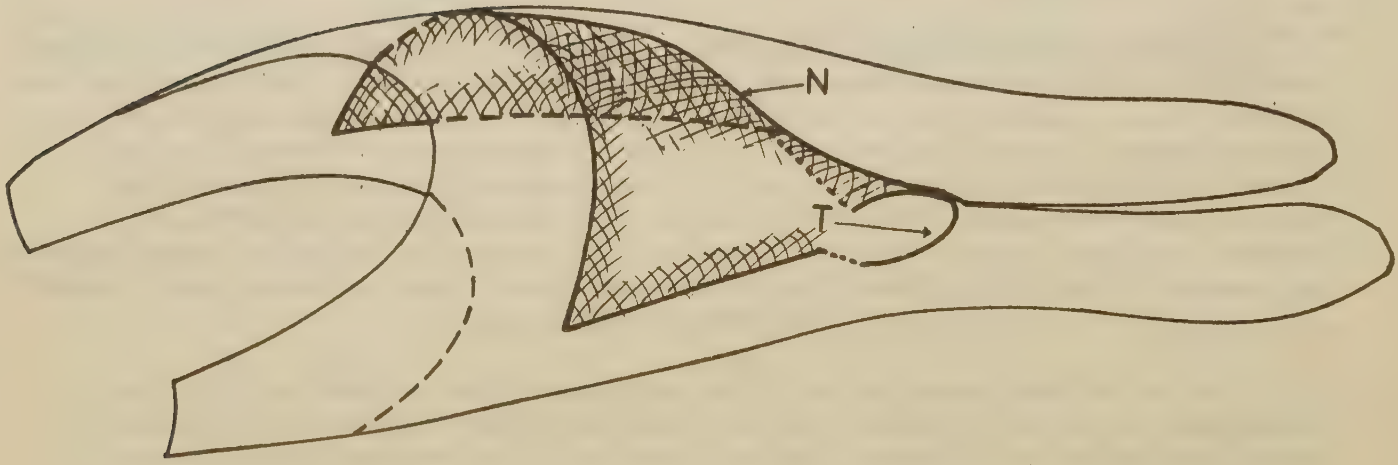

Fig. 2 La nappe intermédiaire (N) dans le chalut sélectif. Le passage (T) vers la poche inférieure est constitué par des coûtures reliant la nappe intermédiaire au ventre

On a pu constater que le poids de crevettes franchissant cette nappe et atteignant la poche supérieure variait, selon les traits, de 75 à 99 pour cent, la moyenne étant de l'ordre de 85 pour cent pour l'ensemble de ces pêches expérimentales faites en 1964 et 1965.

Une perte n'excédant pas 15 pour cent des crevettes ayant pénétré dans le chalut est parfaitement acceptable, compte tenu du nombre d'animaux écrasés par le poids des divers invertébrés ou blessés par les pinces des décapodes nageurs (Polybius Henslowi) souvent fort abondants.

Il faut également tenir compte du gain de temps considérable que représente le tri automatique des crevettes par la nappe intermédiaire.

Il restait à savoir si la crevette rose ou bouquet (Leander serratus (PENN.)) espèce fort prisée en France, se comportait comme la crevette grise et pouvait, par conséquent, être capturée de la même manière.

Les premiers essais ont été faits en février 1964. Ils ont montré que 16 à 36 pour cent (en moyenne 25 pour cent) des crevettes roses n'atteignaient pas la poche supérieure, et de ce fait étaient perdues. Ce résultat médiocre peut s'expliquer partiellement par la grande taille de ces crustacés, qui atteignent 12 cm, alors que les crevettes grises ne dépassent guère 7 à 8 cm. Il faut également noter qu'à l'époque où nos pêches expérimentales ont été faites, les femelles étant pour la plupart chargées d'oeufs, n'étaient guère vivaces; au lieu de sauter à travers la nappe de sélectivité, elles réagissaient mollement et se laissaient souvent entraîner vers le fond du chalut, c'est-à-dire, vers la poche inférieure dont le grande maillage leur permettait de s'échapper.

Nous pensions alors que leurs réactions pourraient se modifier en fonction de leur état physiologique et nous avions prévu que lorsque les femelles seraient libérées de leurs oeufs, un plus grand pourcentage d'entre elles atteindrait la poche supérieure. C'est ce que nous avons vérifié, par la suite, lorsque les femelles n'étant plus oeuvées, nous les avons recueillies dans la poche supérieure du chalut sélectif dans des proportions variant de 80 à 99 pour cent.

Une expérience plus récente (janvier 1967) pour laquelle nous avions légèrement modifié la nappe intermédiaire a confirmé ces résultats.

Pour augmenter les chances de passage de ces grandes crevettes vers la poche supérieure, nous avons utilisé un maillage de 30 mm de côté pour confectionner le tiers postérieur de la nappe intermédiaire, les deux tiers antérieurs restant, comme par le passé, d'un maillage de 25 mm. Nous espérions ainsi amener les crevettes qui n'avaient pas traversé la nappe dès leur entrée dans le chalut, à le faire plus aisément à la fin de leur trajet. Les résultats ainsi obtenus ont été concluants mais la sélectivité de la nappe intermédiaire s'est trouvée réduite, et une quantité accrue de poissons et d'invertébrés a été refoulée vers la poche supérieure à travers les grandes mailles.

Cet inconvénient doit être pallié car il ôte une partie de son intérêt au dispositif qui a pour but d'épargner les jeunes poissons et de réduire le travail du pêcheur en lui évitant un tri long et fastidieux.

Il doit être possible d'y remédier en inversant les maillages de cette nappe, c'est-à-dire en placant à l'avant la nappe en mailles de 30 mm, qui laissera aisément passer les grandes crevettes au moment où elles pénètrent dans le chalut et où elles sont le plus actives, et en réservant à la partie postérieure le maillage de 25 mm qui repoussera vers la poche inférieure les organismes du fond qui représentent souvent un poids très important. Or, l'un des avantages du chalut sélectif réside dans la séparation automatique des crevettes et des captures accessoires dont 72 à 95 pour cent (en poids) sont, grâce à ce système, rejetées vers la poche inférieure.

3 COMPORTEMENT ET PÊCHE DES POISSONS

On sait que le chalutage des crevettes, généralement pratiqué dans la zone côtière entraîne la capture d'assez nombreux poissons. Ces captures, parfois négligeables si l'on n'en considère que le poids, sont le plus souvent importantes quant au nombre des individus. Or, les lieux de pêche des crevettes se trouvent fréquemment dans des zones de concentration d'immatures qui sont ainsi abusivement détruits.

Dans quelle mesure l'utilisation du chalut Devismes peut-il contribuer à améliorer cette situation? Examinons les comportements des poissons capturés sur les lieux de pêche des crevettes et la relation entre ce comportement et leur sauvegarde éventuelle par le dispositif de sélectivité de notre chalut.

3.1. Les poissons ronds

3.1.1. Poissons pélagiques Il n'est pas rare de rencontrer des sardines, sprats, anchois, chinchards, maquereaux, etc... sur les lieux de pêche des crevettes. Lorsque ces poissons séjournent près du fond et qu'ils se trouvent pris dans un chalut, ils ont tendance à nager obliquement en direction de la surface. Ils traversent donc, pour la plupart, la nappe intermédiaire du chalut sélectif, après quoi ils se heurtent aux petites mailles du dos du filet et sont alors dirigés, par la pression de l'eau, vers la poche supérieure.

Le chalut Devismes ne permet donc pas la protection des espèces pélagiques, ce qui est d'ailleurs sans importance, compte tenu des faibles quantités ainsi capturées. Par ailleurs, ces espèces ne sont pas protégées par les Conventions internationales et peuvent donc être pêchées librement.

3.1.2. Poissons de fond D'autres espèces, habituellement pêchées au chalut, se retrouvent en quantités variables dans les secteurs à crevettes. Ce sont principalement les merlans et merlus.

Bien que vivant au voisinage du fond sur lequel ils se nourrissent parfois (c'est le cas du merlan, prédateur des crevettes) ces poissons, bons nageurs, se comportent dans le chalut comme les espèces pélagiques. Ils ont donc tendance à nager vers la partie supérieure du filet et, par conséquent, à traverser eux aussi la nappe intermédiaire. Ce sont, évidemment, les plus grands qui seront arrêtés par cette nappe. Le pourcentage du nombre de poissons ainsi protégés varie donc selon la composition du stock au moment de la pêche. Pour les merlus, le nombre des individus ayant atteint la poche supérieure varie de 0 à 57 pour cent; en moyenne, les deux tiers d'entre eux n'y parviennent pas. Pour les merlans, le pourcentage de poissons recueillis dans la poche supérieure a varié selon les lieux et les époques de 39 à 93 pour cent. La protection de l'espèce ne devient réellement efficace que pour les animaux ayant une taille au moins égale à 20 cm.

3.2. Les poissons plats

Les Hétérosomates sont, à l'inverse de la plupart des poissons ronds, typiquement benthiques. Lorsque le bourrelet du chalut les soulève du fond, ils n'ont pas tendance à s'élever mais au contraire à nager parallèlement au fond. Ils se dirigent donc vers la poche inférieure d'où ils pourront s'échapper si les mailles en sont assez grandes.

C'est ainsi que les deux tiers des soles sont protégés. Une partie d'entre elles, cependant, parvient à traverser la nappe intermédiaire. Ce sont généralement des animaux de moins de 15 cm qui doivent être rejetés vers la partie supérieure du filet lorsqu'ils atteignent le couloir étroit que forment la nappe intermédiaire et le ventre du chalut à l'entrée de la poche inférieure.

Les autres Pleuronectes, plie, flet, limande, turbot, etc... dont la forme est rhomboïdale sont bien mieux protégés que les soles. En effet, dans la quasi totalité des cas, 100 pour cent d'entre eux sont rejetés vers la poche inférieure et ce n'est qu'exceptionnellement qu'on en a dénombré 5 pour cent dans la poche supérieure.

Il n'est pas utile d'insister sur l'ampleur des destructions de poissons immatures causées par les chaluts à crevettes traditionels. On sait, en effet, que chaque jour quelques dizaines de milliers de jeunes poissons sont inutilement capturés dans les secteurs les plus pauvres du golfe de Gascogne; on sait également que c'est par centaines de milliers qu'il faut dénombrer ceux qui sont détruits dans les zones plus riches de la Manche et de la Mer du Nord.

Bien que le chalut Devismes ne puisse empêcher la destruction d'une certaine quantité d'immatures, les taux de protection que nous avons observés, variant selon les espèces des deux tiers à 100 pour cent (à l'exception du merlan) permettent de se faire une idée de la quantité de poissons que l'utilisation d'un tel chalut, peut soustraire à l'action destructrice des pêcheurs côtiers.

4 CONCLUSION

Nous venons de décrire un modèle de chalut qui a été réalisé en tenant compte des comportement des crevettes et des poissons qui peuplent les mêmes secteurs.

Nous avons vu que, non seulement l'expérimentation a confirmé les observations mais encore que l'utilisationde cet engin est bénéfique à divers titres.

1. Il permet de capturer autant de crevettes qu'un chalut ordinaire.

2. Les crevettes étant séparées des organismes benthiques, souvent abondants et pesants, sont de meilleure qualité.

3. Le travail du pêcheur est allégé du fait que le tri des crevettes est déjà partiellement fait par le chalut lui-même.

4. Une quantité très importante de poissons immatures peut être sauvegardée.

Par ailleurs, on a noté au cours de cet exposé que si les poissons plats sont bien protégés par le dispositif de sélectivité, il n'en est pas de même pour certains poissons ronds comme les merlus et surtout les merlans dont le comportement les amène à traverser la nappe de sélectivité.

Il nous a paru possible de tirer parti de cette situation, pour une autre pêche, celle des langoustines (_Nephrops_ _norvegicus_) dont la capture au moyen d'un chalut s'accompagne souvent de prises importantes de jeunes merlus et merlans.

La réglementation française autorisant les pêcheurs à utiliser un maillage de 25 mm de côté dans les poches des chaluts à langoustines (réglementation des "pêches spéciales"), nous avons pensé que si l'on plaçait dans un chalut ordinaire une nappe intermédiaire dont le maillage est de 30 mm, la plupart des jeunes poissons la traverseraient et pourraient s'échapper par une poche supérieure également en grand maillage, tandis que les langoustines qui, en principe, ne doivent pas traverser la nappe sélective seraient recueillies dans la poche inférieure.

Un tel type de chalut a été récemment réalisé par l'Institut scientifique et technique des Pêches maritimes et l'expérimentation en est en cours.

Pour conclure, sur un plan plus général, il nous paraît désormais indispensable que l'étude et la réalisation d'engins de pêche soient faites de façon concomitante avec des études et des observations de comportement des animaux dans leur milieu et confrontées avec ces engins.

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INFLUENCE DU TAUX D'ARMEMENT SUR LA VITESSE DE PLONGÉE DE LA SENNE

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Résumé

L'efficacité de la senne tournante et coulissante dépend en particulier de la vitesse avec laquelle le filet plonge dans l'eau. Cette vitesse de plongée peut être améliorée par une augmentation du lestage de la ralingue inférieure, mais il est parfois plus judicieux de chercher à obtenir cette amélioration au moyen d'un montage plus rationnel du filet.

Après avoir rappelé un certain nombre de définitions et mis en évidence à cette occasion l'importance de la notion de chute pratique, une étude théorique a montré que la traînée hydrodynamique, dont dépend la vitesse de plongée du filet, est influencée par le taux d'armement de ce dernier. A cet égard, les sennes montées à 40 - 60 pour cent doivent plonger plus vite que celles montées à 80 - 90 pour cent.

La comparaison de la senne à thons de type américain et de la senne à harengs de type norvégien, qui représentent deux extrêmes du point de vue du mode de montage, montre que la conception du filet est liée principalement au comportement de l'espèce recherchée.

Des essais sur des maquettes au 1/36ème d'une senne à thon ont permis de vérifier la relation, démontré théoriquement, entre le taux d'armement et la vitesse de plongée.

E/6

INFLUENCE OF HANGING COEFFICIENT ON "DIVING" SPEED OF SEINE NETS

Abstract

The efficiency of a purse seine is governed among other things by the speed with which the net takes up its position in the water. This speed can be improved by adding to the sinkers, though it may be preferable to aim at a more efficient hanging coefficient.

Definitions of certain terms, including the important distinction between theoretic and effective depth, are followed by a theoretic study of hydrodynamic drag, showing that this factor, which governs the rapidity with which the net enters the water, is influenced by the hanging coefficient. Seines with a coefficient of 40 to 60 per cent should thus "dive" faster than those hanging an 80 to 90 per cent coefficient.

A comparison of American tuna seines and Norwegian herring seines, which represent the two extreme approaches to the hanging question, shows how net design is governed primarily by the behaviour of the species fished.

In the course of trials with 1:36 scale models of a tuna seine, the correlation suggested by theory, between hanging coefficient and the speed at which the net reaches the desired depth was verified.

INFLUENCIA QUE EJERCE EL MODO DE ARMAR EL ARTE SOBRE LA VELOCIDAD DE HUNDIMIENTO DE LA RED DE CERCO DE JARETA

Extracto

La eficacia de la red de cerco de jareta depende en particular de la velocidad a que la red se hunde, velocidad que se puede mejorar aumentando el peso de la relinga de plomos, pero a veces conviene hacerlo armando la red de un modo más racional.

Después de haber recordado algunas definiciones y puesto de relieve en esta ocasión la importancia de la noción de caída práctica, un estudio teórico ha mostrado que la resistencia hidrodinámica, de la que depende la velocidad de hundimiento de la red, se halla influida por el modo de armar esta última. A este respecto, las redes de cerco armadas con un coeficiente de 40-60 por ciento, deben hundirse con más rapidez que las armadas con un coeficiente de 80-90 por ciento.

La comparación de la red de cerco de tipo americano para pescar atunes y de la red de cerco de tipo noruego para pescar arenques, que representan dos extremos desde el punto de vista del modo de armarlas, muestra que la red está concebida de arreglo, principalmente, con el comportamiento de la especie que se desea pescar.

Dos ensayos con modelos a escala 1:36 de una red de cerco para pescar atunes han permitido comprobar la relación que existe, demostrada teóricamente, entre el modo de armar el arte y la velocidad de hundimiento.

1 INTRODUCTION

L'efficacité d'une senne tournante et coulissante dépend de nombreux facteurs, parmi lesquels on peut citer en premier lieu les dimensions du filet monté, la rapidité d'encerclement du banc, la vitesse de plongée de l'engin et la durée du virage de la coulisse. Parmi ces facteurs, la vitesse de plongée du filet paraît être un élément très important qui conditionne directement les capacités pêchantes de la senne. En effet, si l'immersion verticale de la nappe ne se réalise pas assez vite, la capture a peu de chances d'être fructueuse, le poisson ayant le temps de s'échapper sous la ralingue de plomb, au lieu d'être arrêté par le mur du filet.

Des mesures effectuées sur une senne à thon à l'aide du bathykymographe, appareil servant à enregistrer la profondeur en fonction du temps, ont montré qu'il fallait environ 4 minutes pour que le filet atteigne les trois-quarts de sa profondeur maximale, celle-ci n'étant atteinte qu'au bout d'une dizaine de minutes (Hester 1961). Ce laps de temps paraît très important en comparaison de la très courte durée (de l'ordre de 3 minutes) de la mise à l'eau du filet, pendant l'encerclement du banc de poissons.

Pour obtenir une plus grande rapidité de plongée de la senne, on est d'abord amené à augmenter le lestage de la ralingue inférieure. Mais cette augmentation de poids se trouve vite limitée par l'encombrement résultant de la nécessité d'accroître corrélativement le volume des flotteurs, qui dépasse déjà 10 m3 sur une senne courante. Il semble donc plus judicieux de chercher à améliorer la vitesse d'immersion en agissant sur le filet lui-même, en particulier dans le mode de montage de l'alèze le long des cordes de liège et de plomb. En effet, certains technologistes ont déjà signalé l'influence que pouvait avoir le "flou" de la nappe, résultant d'un montage à mailles plus ou moins ouvertes, sur cette vitesse. (Hamre 1963, Percier 1966).

Après un rappel de la définition des principaux termes employés pour caractériser le filet et son montage, nous tenterons ici, sur la base à la fois de considérations théoriques et d'essais réalisés sur des maquettes, de préciser dans quelle mesure le mode de montage sur les ralingues, ou armement, peut modifier, au même titre que le lestage, la vitesse de plongée de la senne. Nous essayerons également d'expliquer par le comportement différent des espèces capturées les particularités de montage des principaux types de senne.

2 DEFINITIONS

Dans l'usage commercial courant, une senne tournante et coulissante est définie essentiellement, indépendamment du maillage et du type de fil employé, par la longueur de la corde de liège et par la chute. Si la mesure de la corde de liège correspond bien à la dimension du filet monté, la valeur de la chute correspond en général à la profondeur du filet mailles étirées. Cette dernière dimension est en fait la chute théorique du filet, par opposition à ce que l'on peut appeler la chute pratique du filet monté. La chute pratique est toujours plus faible que la chute théorique, la différence entre ces deux dimensions dépendant du montage avec des mailles plus ou moins ouvertes sur les ralingues de liège et de plomb.

Le mode de montage du filet est caractérisé par le taux d'armement, qui est defini, selon les normes recommandées par l'I.S.O., par un pourcentage E exprimant le rapport de la longueur de la ralingue à celle de la nappe de filet étirée:

$$E\,\% = \frac{\text{longueur du cordage}}{\text{longueur de la nappe de filet}} \times 100$$

E/6

Comme nous le verrons plus loin, le taux d'armement du filet varie en général de 40 à 90 pour cent, suivant les pays, les conditions de pêche et surtout suivant les espèces recherchées.

3 FACTEURS INFLUENCANT LA VITESSE DE PLONGÉE DU FILET. IMPORTANCE DU TAUX D'ARMEMENT

Lorsqu'on file la senne, celle-ci tombe à l'eau, bien allongée, avec toutes ses mailles pratiquement serrées les unes contre les autres. Elle se déploie vers le bas, entraînée dans la profondeur par le poids du lest fixé sur la ralingue de plomb, lest complété accessoirement par les anneaux de boursage et par la coulisse elle-même. La vitesse avec laquelle la nappe coule dépend alors, d'une part, de l'importance relative du lestage et, d'autre part, de la résistance hydrodynamique que la nappe oppose à son déplacement vertical. Il convient de souligner ici que la nappe coule aussi sous l'effet de son propre poids dans l'eau, mais cet effet reste peu important et peut être considéré comme négligeable dans la pratique en raison de la faible densité du nylon (1,14).

On peut rappeler à ce sujet les études publiées par Andreev (1958) qui, poursuivantles travaux de Baranov, a proposé des formules donnant la vitesse de plongée en fonction du poids du lest et du poids du filet dans l'eau. Il semble toutefois que ces formules, établies empiriquement pour des sennes d'un type donné mais sans tenir compte du taux d'armement, ne peuvent pas être appliquées dans tous les cas.

En définitive, deux forces antagonistes principales sont à considérer: le poids du lest et la résistance hydrodynamique de la nappe. Si la première de ces forces est bien connue, la deuxième peut être précisée de la manière suivante: il résulte du déplacement vertical du filet une traînée qui, suivant la loi générale de l'hydrodynamique $R = K\,S\,V^2$, peut être considérée comme proportionelle à la surface de la projection, sur le plan horizontal, des éléments de fils constituant les mailles.

Le déplacement de l'alèze s'effectuant en principe parallèlement au plan du filet et suivant une direction verticale, dans un élément de surface de la senne en position déployée la surface S du fil projetée sur le plan horizontal peut être exprimée par la formule:

$$S = \frac{d}{L} \cdot \frac{1}{\cos\varphi}$$

qui est déduite du produit du nombre de mailles N par élément de surface du filet monté par la surface projetée s de chaque maille.

On a ainsi $N = \dfrac{1}{4\,L^2} \cdot \dfrac{1}{\sin\varphi\,\cos\varphi}$

et $s = 4\,Ld\,\sin\varphi$

D'où l'on tire

$$S = N \,.\, s = \frac{d}{L} \cdot \frac{1}{\cos\varphi}$$

Dans ces formules on désigne par:

d = diamètre du fil

L = dimension du côté de maille

φ = demi-angle d'ouverture de la maille

$\frac{d}{L}$ étant constant, pour une senne d'un type donné, la surface projetée des mailles et, par conséquent, la traînée hydrodynamique du filet pendant son mouvement vertical sont proportionnelles à $\frac{1}{\cos \varphi}$ que nous désignerons par T ou facteur de traînée.

Les variations de T peuvent être représentées par une courbe (Fig. 1), pour des angles d'ouverture des mailles 2φ allant de 20 à 160° , correspondant respectivement à des taux d'armement de 17,4 et 98,5 pour cent. On voit que le facteur de traînée augmente d'une manière continue avec le pourcentage d'armement. Cette augmentation, qui est déjà assez marquée pour les pourcentages voisins de 70,7 pour cent (maille carrée), devient très importante pour les armements de plus de 80 pour cent.

Il convient toutefois de souligner que l'augmentation du facteur T ne fournit que le sens et non la valeur absolue de la variation du temps de plongée; celui-ci dépend en fait de la traînée totale de la nappe qui résulte non seulement de la surface projetée mais aussi du carré de la vitesse.

Il semble donc théoriquement peu judicieux, si l'on veut obtenir la plus grande vitesse de plongée, de monter les sennes à des pourcentages d'armement supérieurs à 80 pour cent. Au contraire, pour augmenter l'efficacité du filet et la rapidité de manoeuvre, il paraît préférable d'adopter un montage de l'ordre de 50 à 60 pour cent. D'autre part ce montage sera d'autant plus valable si la pêche doit s'exercer sur des bancs de poissons nageant à une certaine profondeur, comme c'est le cas pour les sennes à harengs, ainsi que nous le verrons plus loin.

On peut remarquer aussi que, dans la plupart des cas, le montage à 71 pour cent, ou à mailles carrées, est évité, bien qu'il permette de réaliser la plus grande surface de filet monté avec le minimum de mailles. Ce montage présente en effet l'inconvénient de donner une nappe trop plate, peu adaptée à la technique de boursage de la pêche par encerclement. De ce point de vue le montage à 50 - 60 pour cent semble fournir plus de possibilités de boursage que l'armement à 80 - 90 pour cent, dans lequel les mailles très étirées transversalement forment une nappe relativement plus tendue à l'horizontale.

Ceci nous a conduits à préciser la quantité d'alèze utilisée, pour un filet monté de dimensions données, en fonction du taux d'armement adopté. Cette quantité d'alèze est proportionnelle au nombre N de mailles par unité de surface du filet monté qui, comme nous l'avons vu plus haut, est donné par la formule:

$$N = \frac{1}{4\,L^2} \cdot \frac{1}{\sin\varphi\ \cos\varphi}$$

La Fig. 2 montre la variation de N en fonction du taux d'armement. Minimum pour un armement à 71 pour cent correspondant à la maille carrée, ce nombre augmente d'abord lentement, puis très rapidement pour toutes les valeurs du taux d'armement supérieures ou inférieures. Dans la pratique il semble peu rationnel d'envisager de monter un filet à des pourcentages d'armement extrêmes, inférieurs à 40 pour cent ou supérieurs à 90 pour cent (correspondant respectivement à des angles d'ouverture des mailles de 48° et 128°).

L'étude du taux d'armement ne doit pas faire oublier les autres facteurs qui peuvent aussi modifier la vitesse de plongée de la senne. En plus du lestage qui, rappelons-le, est limité pour des raisons de manutention, on peut citer les dimensions des maillages, le diamètre et la nature des fils, le type d'alèze (avec ou sans noeuds) ainsi qu'éventuellement la coupe de la bordure inférieure du filet. En ce qui concerne les maillages et les diamètres des fils, la formule établie précédemment pour la détermination du facteur de traînée vérifie et confirme l'observation pratique dans laquelle il apparaît que le temps de coulée est d'autant plus faible que les maillages sont plus grands et que les fils sont plus fins.

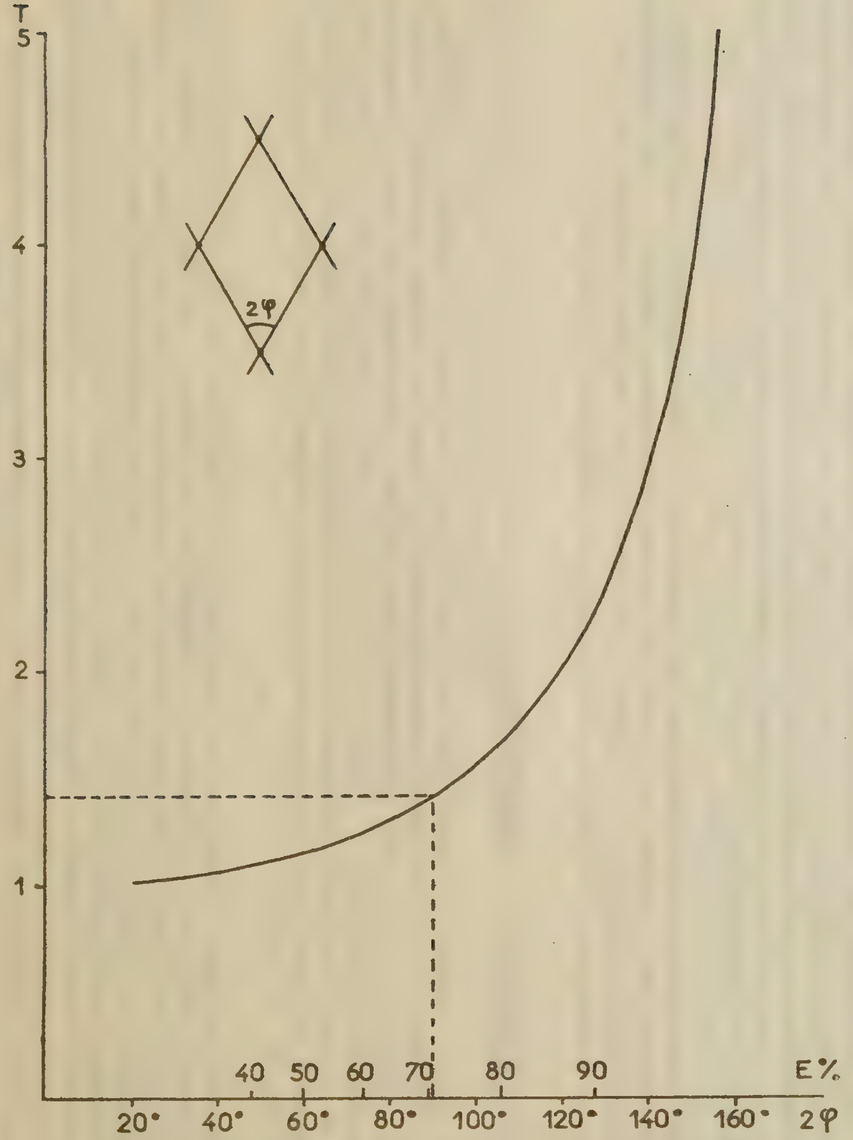

Fig. 1 Variation du facteur de traînée T en fonction du taux d'armement E de la nappe de filet ou de l'angle d'ouverture des mailles 2φ. Les pointillés correspondent à la maille ouverte au carré.

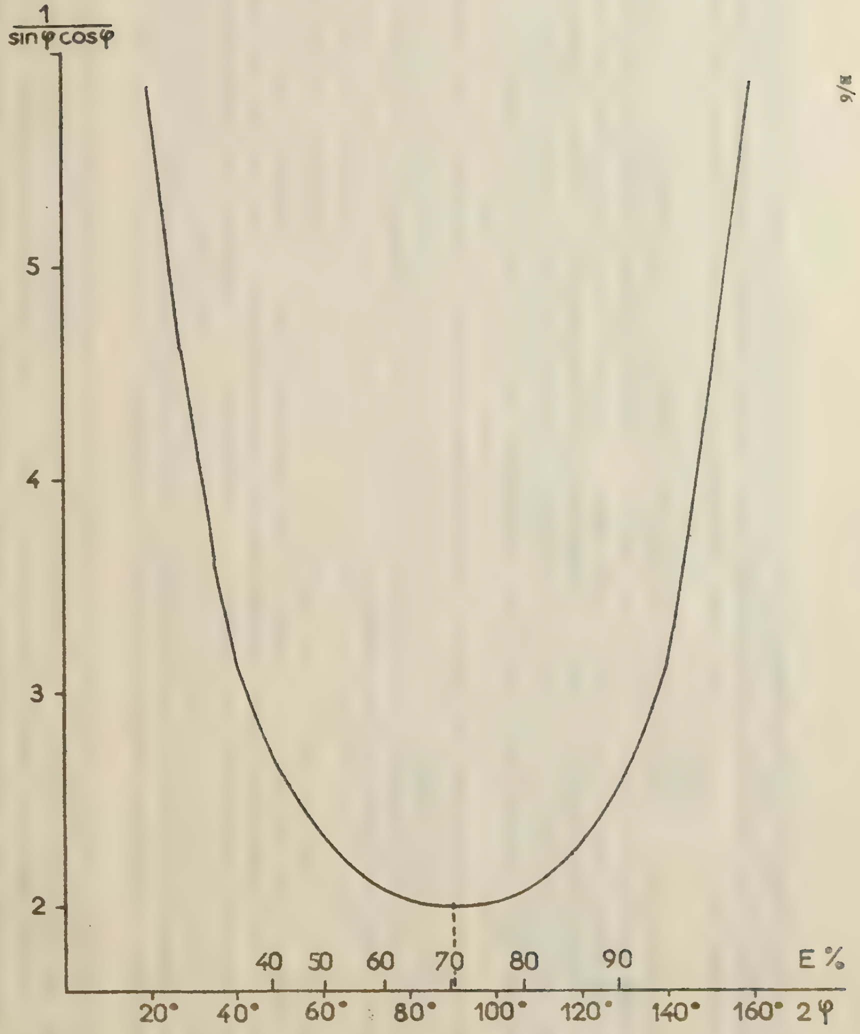

Fig. 2 Relation entre le nombre de mailles par unité de surface du filet monté (exprimé ici par le facteur $\frac{1}{\sin\varphi \cos\varphi}$) et le taux d'armement E ou l'angle d'ouverture des mailles 2φ. Le minimum correspond à la maille carée (E = 70,7 pour cent et 2φ = 90°).

4 COMPARAISON DES PRINCIPAUX TYPES DE SENNES

Cette comparaison sera limitée à deux sortes d'engins: la senne à thon type américain et la senne à hareng type norvégien ou islandais; ils correspondent à deux conceptions nettement opposées qui trouvent en partie leur justification dans le comportement différent des deux espèces exploitées.

La senne à thon américaine est un filet relativement long, présentant une faible chute pratique (celle-ci est, par exemple, de 45 m pour une longueur de 700 m, soit un rapport de l'ordre de 1/15). Monté habituellement selon un taux d'armement moyen de 90 pour cent, ce filet a une faible vitesse de plongée, mais en raison de l'élasticité de l'alèze, très étirée transversalement, il a la possibilité de bourser facilement dans le plan vertical. En contrepartie il est de ce fait particulièrement sensible au courant. Ce type de filet semble surtout efficace dans les eaux à thermocline bien marquée et peu profonde. Préférant les eaux chaudes superficielles, les thons, en général, n'essayent pas de plonger sous la zone de contraste thermique. Toutefois, et ceci est une conséquence de la conception même du filet, si l'on opère dans une région où les conditions hydrologiques ou le comportement de l'espèce ne sont pas ceux qui viennent d'être énoncés, il faut s'attendre à une certaine fréquence d'échecs. La chute pratique et la vitesse de plongée de la senne à thon américaine apparaissent donc perfectibles, ainsi que le montrent les mesures réalisées par Hamre sur la senne à thon norvégienne.

Employée le plus souvent dans des eaux à faible contraste thermique, la senne à hareng norvégienne est caractérisée par sa longueur modérée et surtout par son grand développement vertical. La chute pratique atteint couramment 110 et même 135 m; elle correspond en moyenne au 1/4 de la longueur du filet (440 à 540 m). Cette senne est conçue essentiellement en vue d'une plongée profonde et rapide permettant de capturer les bancs de harengs à la plus grande distance possible de la surface. C'est ainsi que des captures de bancs localisés à 60 - 70 m de profondeur sont fréquemment signalées. A l'inverse de ce qui se passe pour le thon, nous avons affaire ici à une espèce qui effectue des migrations verticales fréquentes, atteignant ou dépassant la profondeur de 300 m. En rapport avec la grande rapidité d'immersion requise, le taux d'armement de la senne norvégienne est beaucoup plus faible que celui de la senne à thon (50 - 55 pour cent au lieu de 90 pour cent).

5 ESSAIS SUR MAQUETTES

Afin de vérifier le bien fondé des considérations théoriques sur la relation qui lie le taux d'armement au facteur de traînée, deux maquettes au $1/36^e$ d'une portion centrale d'une senne à thon de 50 m de chute pratique ont été réalisées. Présentant la même longueur (4 m) et des chutes pratiques identiques (1,40 m), ces deux maquettes ont été montées avec des taux d'armement bien distincts de 53 et 85 pour cent. Le diamètre du fil et le maillage du filet nylon, ayant servi à confectioner ces deux modèles, correspondait exactement, après réduction au $1/5^e$, à ceux de la senne grandeur normale (mailles de 11 mm et fil de Ø 0,46 pour 50 mm et 2,09 mm). De cette manière, la surface projetée du fil, qui conditionne la traînée hydrodynamique, se trouve réduite suivant la carré de l'échelle de réduction linéaire.

Le choix des pourcentages d'armement des deux filets à comparer présentait par ailleurs l'avantage de correspondre exactement, pour une même longueur et une même chute pratique, à un nombre total de mailles identique. L'influence des forces de viscosité, qui auraient pu fausser la comparaison se trouvait donc éliminée. Pour la même raison les poids dans l'eau des deux filets étaient rigoureusement semblables.

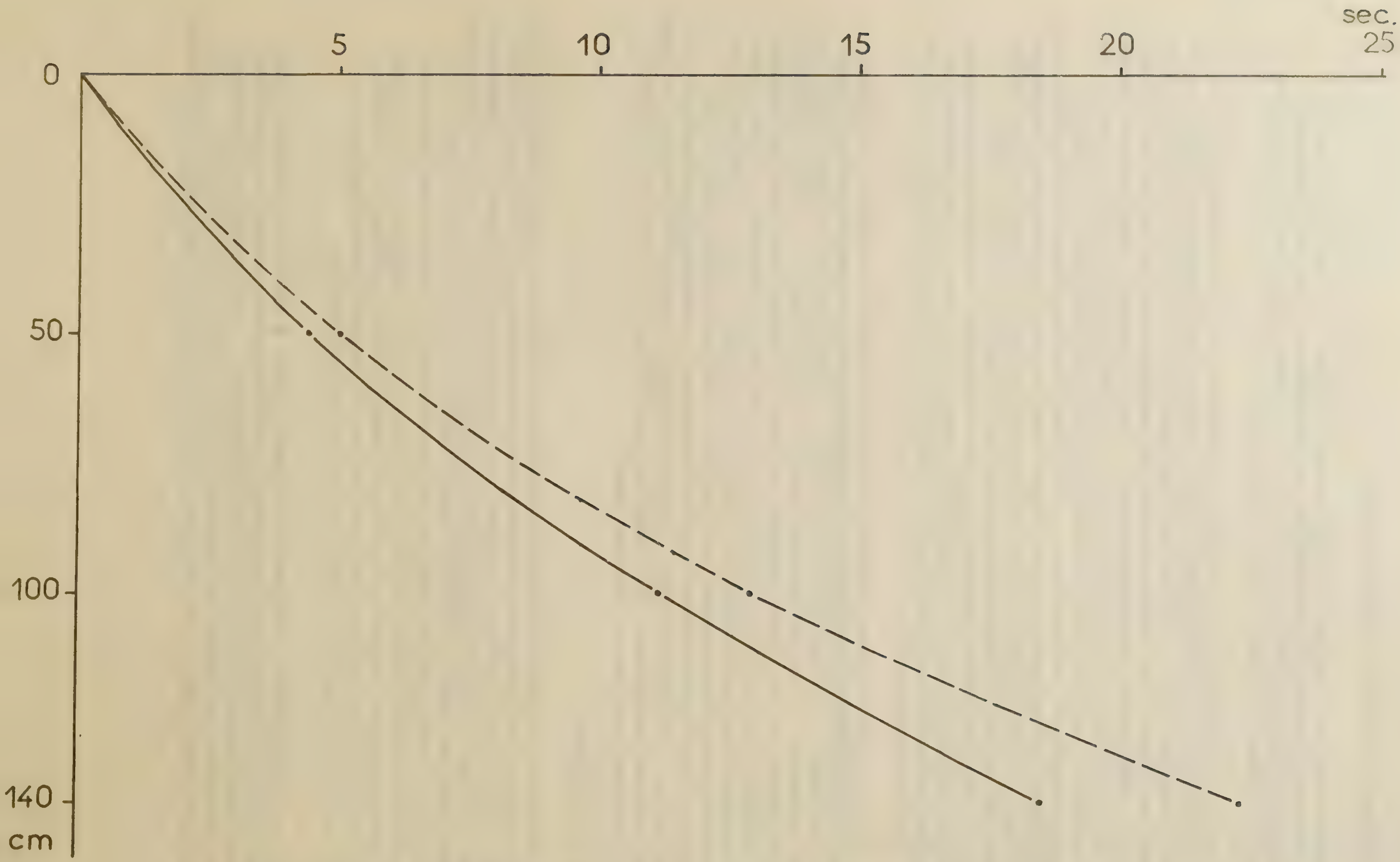

Fig. 3 Courbes donnant la profondeur d'immersion (en cm) en fonction du temps (en secondes) d'après des observations réalisées sur deux maquettes de sennes. Le trait plein correspond à un filet monté à 53 pour cent et le trait interrompu à un filet de dimensions identiques mais monté à 85 pour cent.

Représentant la force qui doit vaincre la traînée qui résulte de la surface du filet, le lestage des maquettes aurait dû normalement être égal à 60 g par m2 de filet monté; il aurait été ainsi équivalent à un lest moyen de 3 kg par mètre de corde de plomb et la vitesse du filet grandeur normale. Pour des raisons de facilité d'observation, la vitesse de plongée des modèles a été réduite grâce au choix d'un lestage plus faible (8 g par m2).

Au cours des essais effectués en bassin, les temps de passage des ralingues de plomb des maquettes aux profondeurs de 0,50 et 1,00 m, ainsi que le temps nécessaire à l'obtention de la chute maximale ont été notés. Les moyennes de plusieurs séries d'observations nous ont permis de tracer les courbes donnant la profondeur d'immersion des deux filets modèles réduits en fonction du temps (Fig. 3). Les courbes obtenues montrent bien que la senne montée à 85 pour cent coule plus lentement que la senne à 53 pour cent, l'accroissement du temps de plongée étant respectivement de 14, 16 et 21 pour cent aux niveaux 0,50, 1,00 et 1,40 m.

Bien que ces résultats n'aient pas de signification en valeur absolue, ne seraitce qu'en raison de l'échelle de réduction importante, ils n'en constituent pas moins une vérification de nos considérations théoriques et confirment aussi les observations d'Hamre sur la senne à thon norvégienne.

Par ailleurs, pendant ces essais en bassin, nous avons pu apprécier la grande sensibilité au courant, même très faible, du filet monté à 85 pour cent. Cette sensibilité paraît accentuer le ralentissement de la plongée du filet.

6 CONCLUSION

Cette étude a permis de montrer d'une manière théorique, ainsi que par des observations sur maquettes, l'influence du taux d'armement sur la vitesse de plongée de la senne.

Une grande rapidité d'immersion constituant un facteur primordial de l'efficacité de ce type d'engin, en particulier dans le cas de la pêche d'espèces très mobiles, il semble préférable d'une manière générale d'employer un taux d'armement faible, de l'ordre de 50 à 60 pour cent. On obtiendra ainsi une meilleure vitesse de plongée sans avoir à augmenter le lest.

La notion de chute pratique a été mise en évidence. Elle correspond à une caractéristique importante de la senne dont l'utilisateur doit tenir compte lors de la commande de son matériel.

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AN ECHO COUNTING SYSTEM FOR DEMERSAL FISHES

by

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Abstract

A digital data acquisition system for direct counting of echoes from demersal fish containing swimbladders is described. The promising results obtained in initial field tests suggest the system will have application as an effective research tool in population studies.

DISPOSITIF DE COMPTAGE DES POISSONS DE FOND AU MOYEN DES ULTRASONS

Résumé

La communication décrit un système numérique d'acquisition des données permettant le comptage direct des échos provenant de poissons démersaux à vessie gazeuse. Sur la base des résultats prometteurs obtenus lors des premiers essais sur les lieux, il semble que le dispositif puisse fournir un efficace outil de recherche pour les études sur les populations.

CONTADOR DE ECOS DE PECES DEMERSALES

Extracto

Se describe un sistema digital de adquisición de datos para contar directamente los ecos de peces demersales que tengan vejigas natatorias. Los prometedores resultados obtenidos en las pruebas iniciales indican que el sistema podrá aplicarse como instrumento eficaz de investigación en los estudios sobre poblaciones.

1 INTRODUCTION

The need for a better method of assessing fish population abundance and availability has led to the investigation and eventual design of a digital data acquisition system for direct counting of echos from demersal fish containing swimbladders. By using a high power transmitter with a short pulse length and a towed transducer, a system has been designed and tested which counts the number of echos per sound transmission in the last 3.8 m to bottom. The echos are received by a special amplifier and, when they meet the preset requirement of amplitude, are converted to digital pulses, delayed and gated with the transmitted pulse and bottom echo. This allows the bottom echo to be used as a reference. The readout is displayed on an electronic counter and also recorded on punched tape along with other parameters such as depth of water, distance of body from bottom, bottom temperature, Decca position and time. In this paper we will be concerned mainly with the design of the counting system and its possible use as a research tool in population studies.

2 EQUIPMENT AND PROCEDURE

A basic block diagram of the overall counting system can be seen in Fig. 1.

The main components are the transmitter, cable and transducer, preamplifier and measurement amplifier, digital logic and electronic counter. The information is fed into a scanner along with the other parameters and recorded on punched tape.

2.1 Transmitter and transducer

The transmitter used was a modified 3 kw Simrad unit with a frequency of 36.0 khz and a transmitted pulse length of 400 microseconds. 36.0 khz was chosen because of transducer characteristics rather than any acoustic effects. By using this frequency an acoustic pulse was obtained with a rise-time of 100 microseconds compared to 300 microseconds at 38.2 khz, the standard frequency of the sounder. This was of course sacrificing 2.0 db of acoustic pressure. The pressure level at 1 m was recorded at +120 db re 1 u bar. The transducer, a 10 x 32 cm unit, was installed in a 4 ft (1.2 m) "Braincon" V-fin and connected to 600 ft (182 m) of 0.376 in (9.4 mm) cable. The last 300 ft (91 m) was faired. The V-fin, as a vehicle, has three main advantages.

(i) The transducer was decoupled from the ship eliminating a prime source of sonic interference.

(ii) It enabled the experimenter to pick the distance he wished to be above bottom and in so doing control the bottom area covered by the beam.

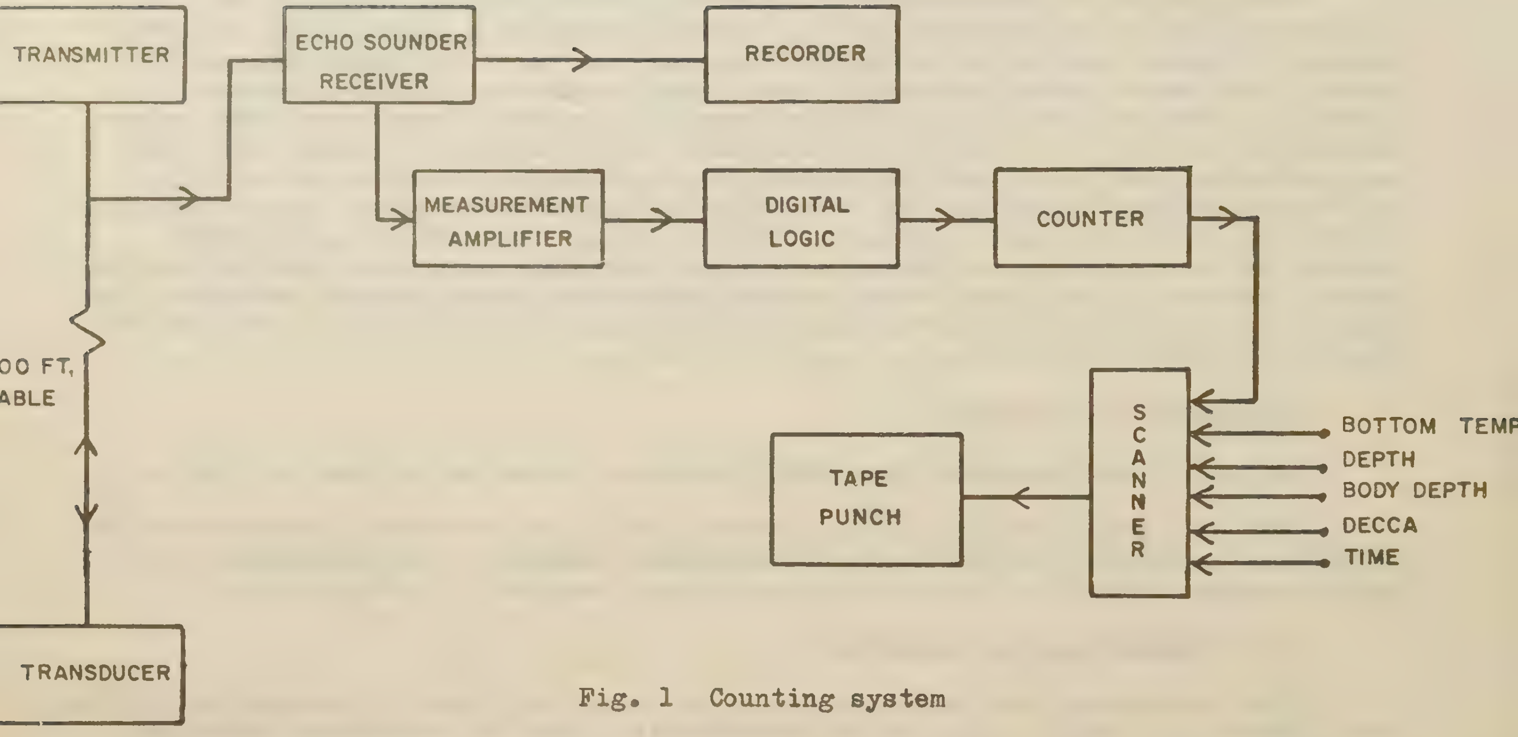
(iii) The stability of the transducer was greatly improved.

2.2 Receiver

The receiver consisted of two stages. The preamplifier of the echo sounder and a special 0-80 db measurement amplifier. The preamp had a maximum gain of 35 db variable from 20 to 35 db. The 80 db amplifier was variable by 10 db steps. The bandwidth of both units was set at 8 khz with center frequency of 36 khz. The increased bandwidth improved the echo shape, that is, it reduced pulse stretching due to the electronics, and increased the rise-time of the echo.

2.3 Digital logic

The logic circuits used are of the type shown in Fig. 2. This represents a circuit board containing two Schmitt Triggers each having a choice of five inputs and trigger levels variable from 0.02 v to 10 v. Larger triggering levels can be obtained by connecting external resistors in the appropriate places. This unit can be


TRANSMITTER
ECHO SOUNDER RECEIVER
RECORDER
MEASUREMENT AMPLIFIER
DIGITAL LOGIC
COUNTER
OO FT,
ABLE
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BOTTOM TEMP
DEPTH
BODY DEPTH
DECCA
TIME
TAPE PUNCH
TRANSDUCER

Fig. 1 Counting system

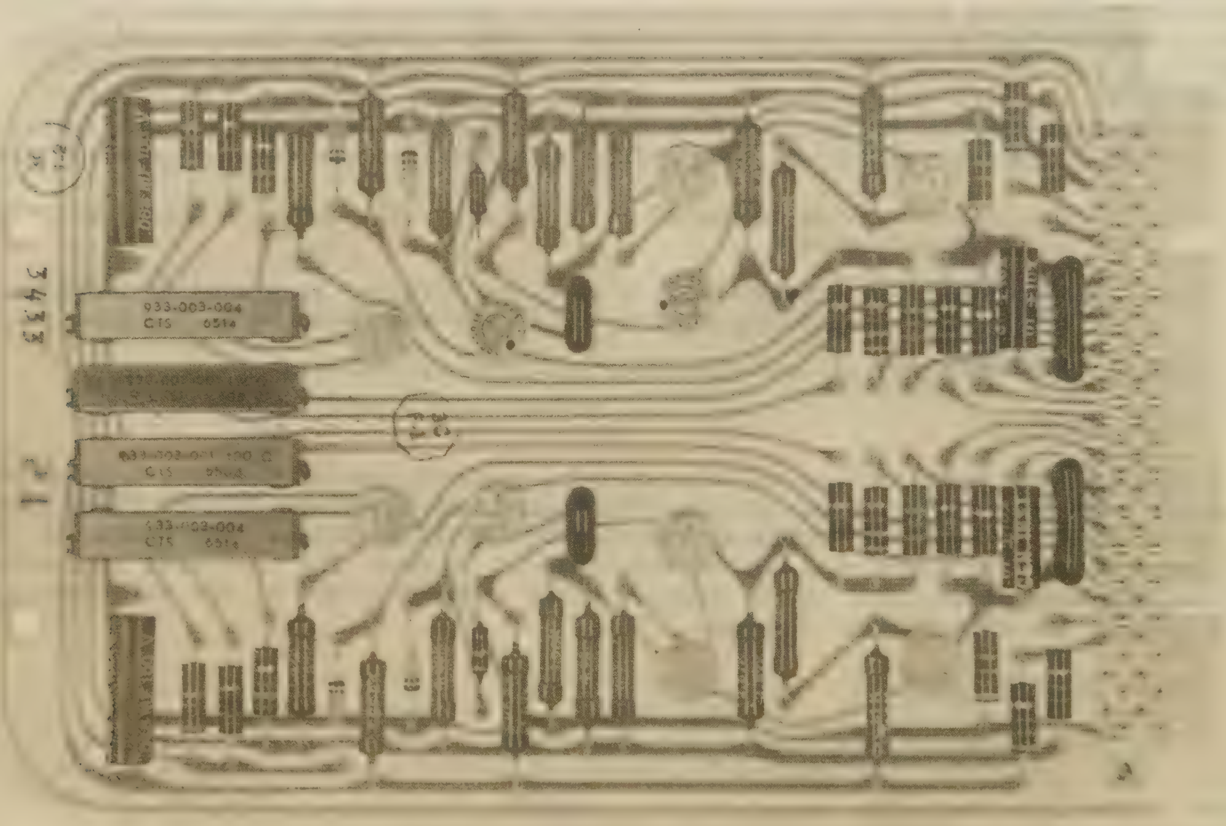

Fig. 2 Schmitt trigger

switched at a rate of 1 megacycle and is typical of the modules used. The system employs negative logic with the voltage levels for logic 1 - 6v, and logic zero 0v.

The digital logic contains three main circuits as shown in Fig. 3. The first having a trigger level of .5v, is for the received echo. The pulse formed from the echo has a duration of 300 microseconds. The unit is then disabled for another 300 microseconds which allows sampling to reoccur 600 microseconds after the initial trigger. The 300 microsecond pulses are then delayed for 6,000 microseconds in order to position the echos from the water volume sampled to a time later than the undelayed bottom echo. Circuits 2 and 3 with trigger levels of 10v (bottom echo) and 6v (transmitter gate) are used for control of the gate sequence. The output NAND gate required all inputs to be at logic one in order to obtain an output.

A graphic representation of the pulse sequence can be seen in Fig. 4. Circuit 1 is switched for every echo above 0.5v. Circuit 2 is switched on reception of the bottom echo and remains on for 5 milliseconds (representing a distance of 3.8 m). Circuit 3 is switched on after a delay which is set depending on the amount of interference in the upper layers. The amount of delay commonly used was 50 milliseconds. Circuit 3 is reset at the end of the 5 millisecond bottom pulse.

3 RESOLUTION

The system was designed to obtain maximum resolution possible with the frequency and pulse length used. The choice of 400 microseconds was practical since the pulse stretching due to the electronics and transducer remained constant and little was gained by going to 200 microseconds. A gate time of 600 microseconds was set to allow 200 microseconds for this stretching. With gating, which allows a scan for 5 milliseconds (3.8 m), this gives a maximum count per transmission of nine echos. The minimum separation distance required for detection of two targets was 25 cm.

The tabulation of data, as was mentioned before was on punched paper tape. The parameters such as depth and count were recorded for every transmission. The decca and time were recorded at 20 min intervals. The data acquisition system with punched tape, is capable of recording 110 characters per second. Six characters are required for each parameter.

4 CALIBRATION

In order to establish that the count is representative of the fish in the sample area, the correlation between echo counts and catch was examined. In earlier phases of development, experiments were conducted on the fishing grounds using an otter trawl and a hull mounted transducer. In order to keep the paths of the net and the ship in line, tows were made in a straight line, following the wind and during periods when ship's roll was at a minimum. The amount of gain used for all tows at a given depth was chosen from data gathered on a series of preliminary tows and was set so that echo count corresponded with the count of fish larger than 25 cm. Once a gain level was chosen it was maintained for the remaining tows at that depth and only these additional tows were used to establish the relation between catch and count. Fig. 5 shows a typical plot for catch vs count. The catch per tow data are for the number of fish over 25 cm in length. The count represents the sum of counts recorded during the tow, corrected for the overlap of the acoustic beam. Overlap could be determined from Decca navigation fixes which gave accurate measures of towing speed during fishing time. The plot consists of a total of 26 one-half hr tows made during a cruise on the Scotian Shelf in November 1966. Calculation of the correlation coefficient between catches and counts resulted in the value of $r = 0.69$; use of the log - log plot as in Fig. 5 reduced the scatter and gave $r = 0.84$. Both correlation coefficients are significant at 5 percent level.

E/7

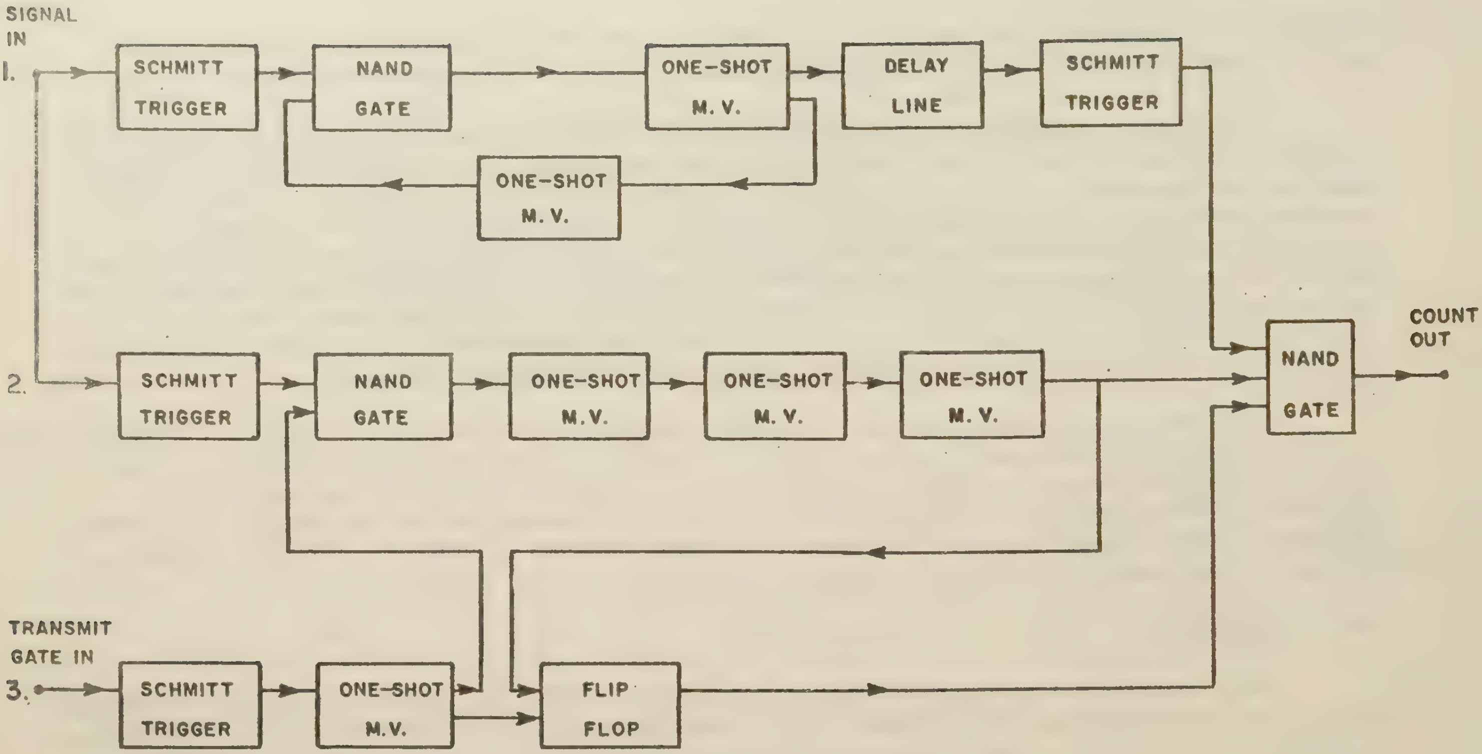
SIGNAL IN
1.
SCHMITT TRIGGER
NAND GATE
ONE-SHOT M. V.
DELAY LINE
SCHMITT TRIGGER
ONE-SHOT M. V.
2.
SCHMITT TRIGGER
NAND GATE
ONE-SHOT M. V.
ONE-SHOT M. V.
ONE-SHOT M. V.
NAND GATE
COUNT OUT
TRANSMIT GATE IN
3.
SCHMITT TRIGGER
ONE-SHOT M.V.
FLIP FLOP

Fig. 3 Logic diagram

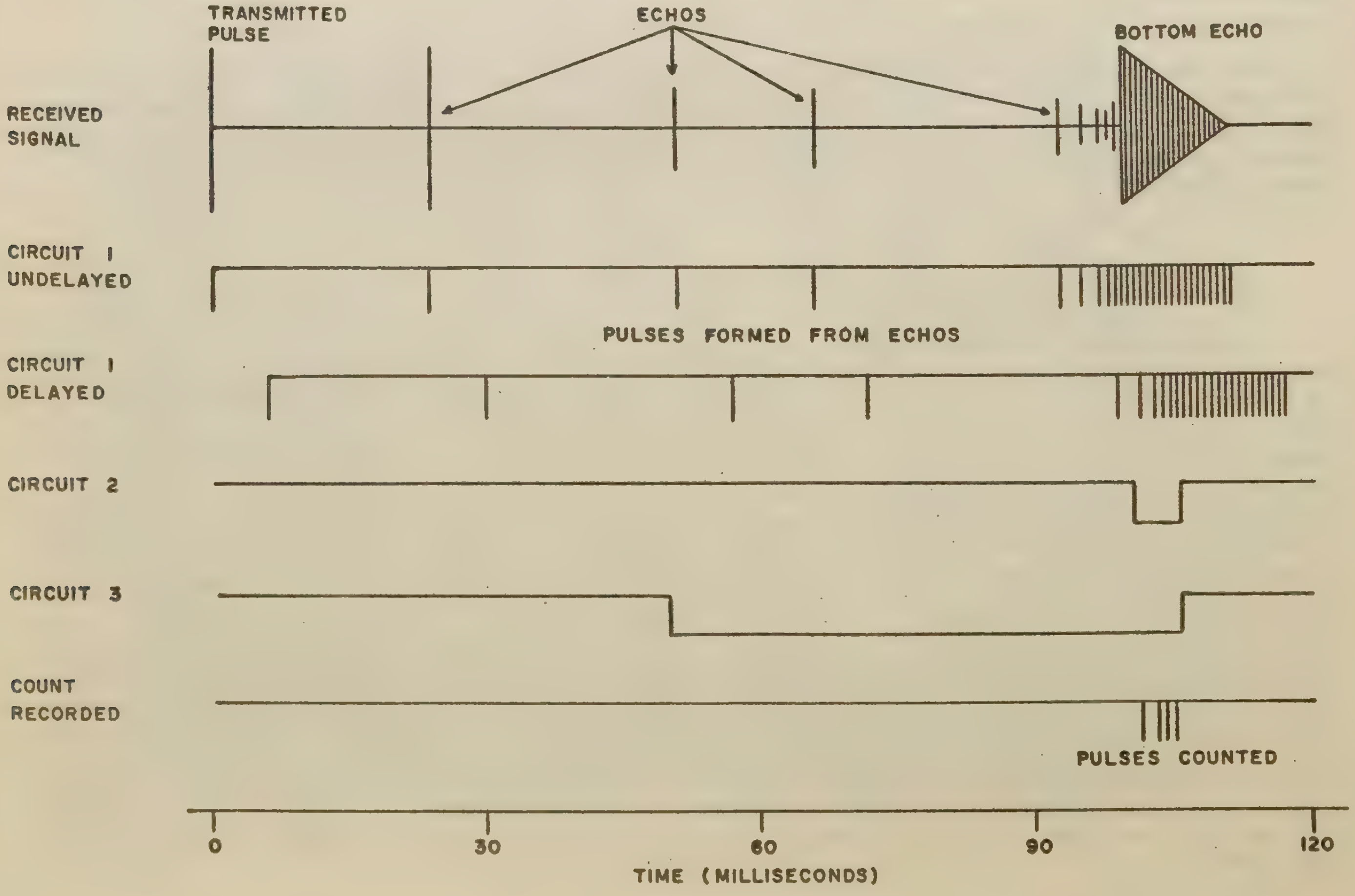

Fig. 4 Pulse sequence

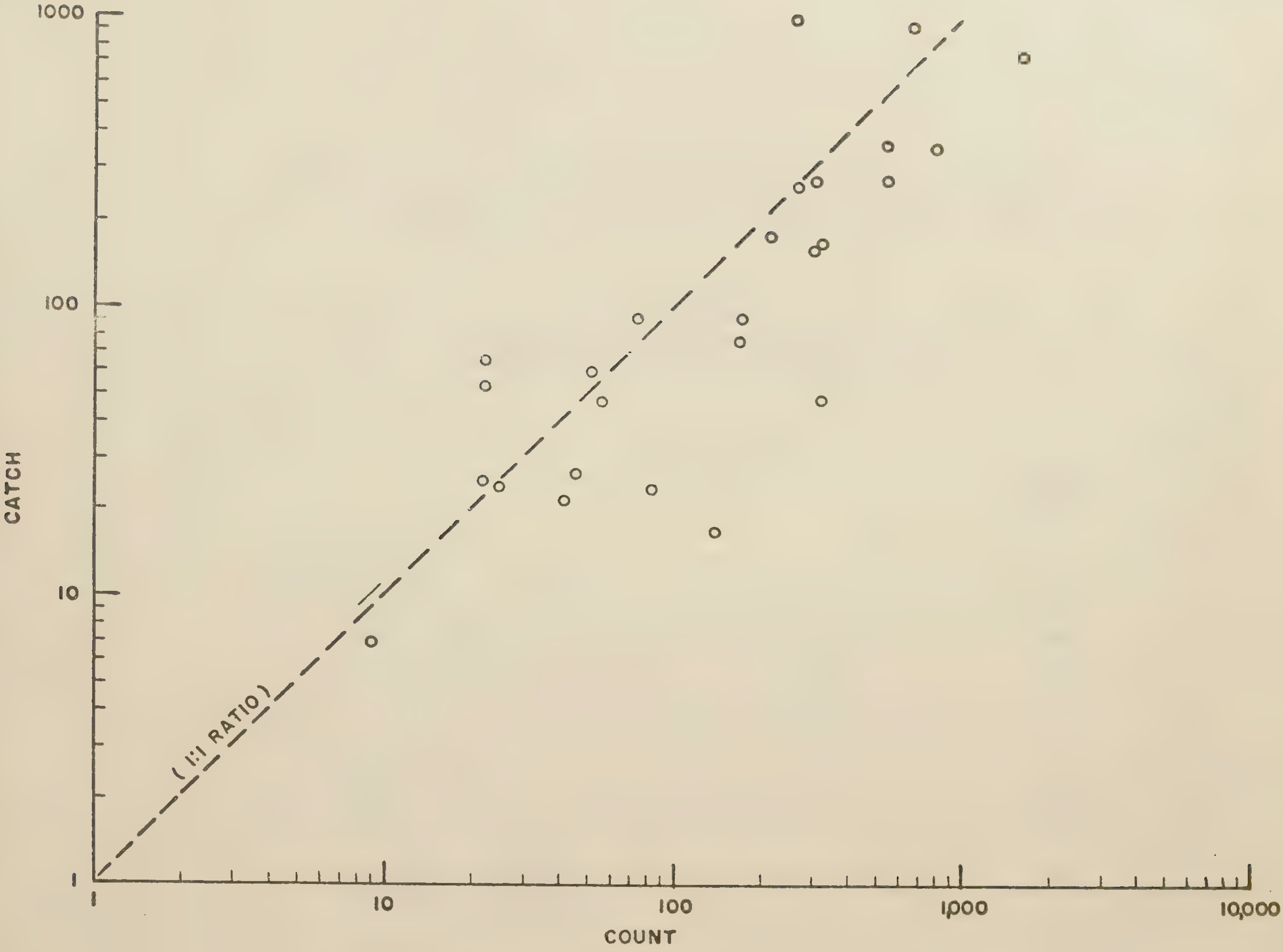

Fig. 5 Typical plot for catch vs count

5 CONCLUSION

The system described shows promise of being of considerable assistance to the researcher interested in population dynamics.

Since it is known that there are variations of catching rate within tow distance which appears to be related to the aggregating behavior of fish, the addition of the acquisition system allowed the data to be tabulated for every transmission enabling the researcher to obtain better definitions of the distribution of these fish.

The punched tape records which contain fine data structure, enable him to study, by using a computer, both overlapped and non-overlapped transmissions and to establish formats for future surveys.

* * * * * * *

ORIENTATION OF JUVENILE ATLANTIC HERRING (Clupea harengus harengus L.) TO TEMPERATURE AND SALINITY

by

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Abstract

Laboratory experiments were conducted on the temperature and salinity preferences of juvenile herring. Prior adaptation to different temperatures produced significant but transient changes in the temperature preference. A final temperature preferendum of 12°C was established. At low temperature (below 10°C) salinities above 29 o/oo were preferred. The response to salinity at temperatures above 10° was not consistent, and appeared to vary seasonally.

E/8

REPONSE DES FORMES JUVENILES DE HARENG DE L'ATLANTIQUE (*Clupea harengus harengus* L.) A LA TEMPERATURE ET A LA SALINITE

Résumé

La communication fait état d'expériences de laboratoire sur les préférences de formes juvéniles de hareng en matière de température et de salinité. L'adaptation antérieure à diverses températures provoque des modifications significatives, mais de courte durée, dans les préférences thermiques. En définitive, une zone de prédilection s'est établie entre 12 et 13°C. Aux basses températures (inférieures à 10°C), les animaux préfèrent les eaux d'un taux de salinité supérieur à 29 o/oo. Au-dessus de 10°C, la réaction au degré de salinité n'est pas uniforme, et semble varier suivant la saison.

ORIENTACION DEL ARENQUE JUVENIL DEL ATLANTICO (*Clupea harengus harengus* L.) A LA TEMPERATURA Y LA SALINIDAD

Extracto

Se realizaron experimentos de laboratorio sobre las preferencias del arenque juvenil en cuanto a temperatura y salinidad. La previa adaptación a distintas temperaturas produjo cambios notables pero pasajeros en la preferencia por la temperatura. Se estableció una preferencia de temperatura definitiva de 12 a 13°C. A temperaturas bajas (inferiores a 10°C) prefieren salinidades superiores a 29 o/oo. La reacción a la salinidad a temperaturas superiores a 10° no fue uniforme, y parece variar estacionalmente.

1 INTRODUCTION

The "sardine" fishery of Maine and the Canadian Maritime Provinces depends on the annual appearance of schools of immature Atlantic herring (Clupea harengus harengus L.) close to shore. Proximity of the herring to the shore is necessary for the effective operation of the commonly used fishing gear : the stop seine and the fixed weir. Purse seines and gillnets have not been used extensively in the sardine fishery. Although the seasonal movements of the young herring are not known in detail, the schools appear more or less regularly in shallow, inshore waters during the spring, summer and autumn. This behavior is sufficiently undependable, however, to create a serious problem for the industry. Failure of the schools to appear within a few hundred meters of the shore reduces their availability to the fishing gear, and thereby reduces the catch, which fluctuates strongly from year to year and from place to place.

The causes of these seasonal aggregations or of their absence can easily be speculated upon, but facts are lacking. Herding by predators, passive transportation by movements of the water mass, attraction to concentrations of food organisms, and responses to hydrographic conditions have all been suggested as reasons for the migration-like behavior. Any, or all of these factors may be contributory, and to some a particular kind of response can reasonably be expected. For example, it is very likely that the fish would tend to avoid predators and be attracted toward food. As for other factors, however, we have no knowledge about the response to be expected. Are herring repelled or attracted by water of a higher or lower temperature than that in which they happen to be? What would be their response to lower or higher salinity? Unexplained behavior of herring is often attributed to temperature or salinity, but the manner of operation may be merely inferred from the circumstances of any particular observation. Although ample evidence is available that temperature especially influences the behavior of herring, much of it is circumstantial. When no real knowledge about the responses of herring to temperature is available, it is easily possible to tailor a temperature-oriented hypothesis to fit almost any observed behavior.

Evidence for a relationship between temperature and herring behavior is abundant in the literature dealing with the eastern Atlantic and Scandinavian stocks. The congregations of Atlanto-Scandian herring at the edge of the "polar front" of cold water described by Devold (1961) is now a "well-known" phenomenon (Blaxter and Holliday 1963). The behavior of herring in relation to the thermocline has been described but not clearly defined. Schubert (1950) reported that the herring would not pass through a thermocline in their vertical migrations if the gradient was as steep as 6°C in 3m; Richardson (1952), on the other hand, felt that the thermocline did not act as a barrier to upward migration, but did note that the fish congregated immediately above it. Postuma (1957) argued that the thermocline determined the depth of the nocturnal upward migration in this way : he noted that the herring occupied that stratum of water between the top of the thermocline and the layer of homogeneous water above it, coming to the surface only when the thermocline began at the surface. Biryukov's (1958) results implied a reciprocal phenomenon in the daytime : that the depth to which the herring descended was between the bottom of the thermocline and the homogeneous water below it.

A partiality toward cold water is suggested by the observations of several investigators. Dietrich, Sahrhage and Schubert (1959) stated that in summer and autumn herring in the North Sea occupy the cold bottom water and the colder this water is, the longer the herring remain there. Devold (1961), in addition to his remarks about herring concentrations along the "polar front", further stated that off northern Norway, herring which elsewhere would have migrated toward the East Icelandic Current in the autumn, move inshore where cooling has begun. Leim, Tibbo and Day (1957) showed an apparent relationship between the cooling of the water in the Gulf of St. Lawrence and an increase in herring catches. It would be difficult to interpret all of these observations in terms of temperature responses, even if these responses were known in detail. One can only assert that in one way or another temperature seems to play a significant role in the movements of herring. Obviously more specific information is needed on the responses of herring to temperature.

Laboratory studies of the effects of temperature or salinity on herring after metamorphosis are scarce. Blaxter and Holliday (1958) observed that herring in captivity ceased to feed at temperatures below 4°C, although other observers have noted feeding at a reduced rate as low as 1°C (Farrin, Scattergood and Sindermann 1957; Blaxter and Holliday 1963). Brawn (1960a) established the upper lethal temperature for "unacclimatized" herring at 19 to 20°C; Kamshylov and Gerasimov (1960) placed the lower lethal extreme at -1.5°C. The effects of sub-lethal temperature variations on behavior have been less well investigated, although in the natural environment most of the temperatures lie within the tolerance limits. Shelford and Powers (1915) tried to demonstrate the temperature preferences of Pacific herring (Clupea harengus pallasi) in a gradient tank. Although the results were inconclusive, they did note an apparent ability of the species to detect temperature differences of 0.6°C. Kamshylov and Gerasimov (1960) observed that young herring would not swim from water at 4.2°C to water of 1.8°C in a tank.

Tolerance of herring to extremes of salinity were investigated by Holliday and Blaxter (1961) and by Brawn (1960b); the range of tolerance was relatively broad, exceeding, as with temperature, the range likely to be encountered in the herring's natural environment. Nothing appears in the literature to show preferences within the tolerance range, however. Some circumstantial evidence which suggests preference was recorded by Rogalla and Sahrhage (1960) who stated that herring avoid the cold bottom water of the Skagerrak when it is of Baltic origin (low salinity) but are found in it during the winter when it is of Atlantic origin.

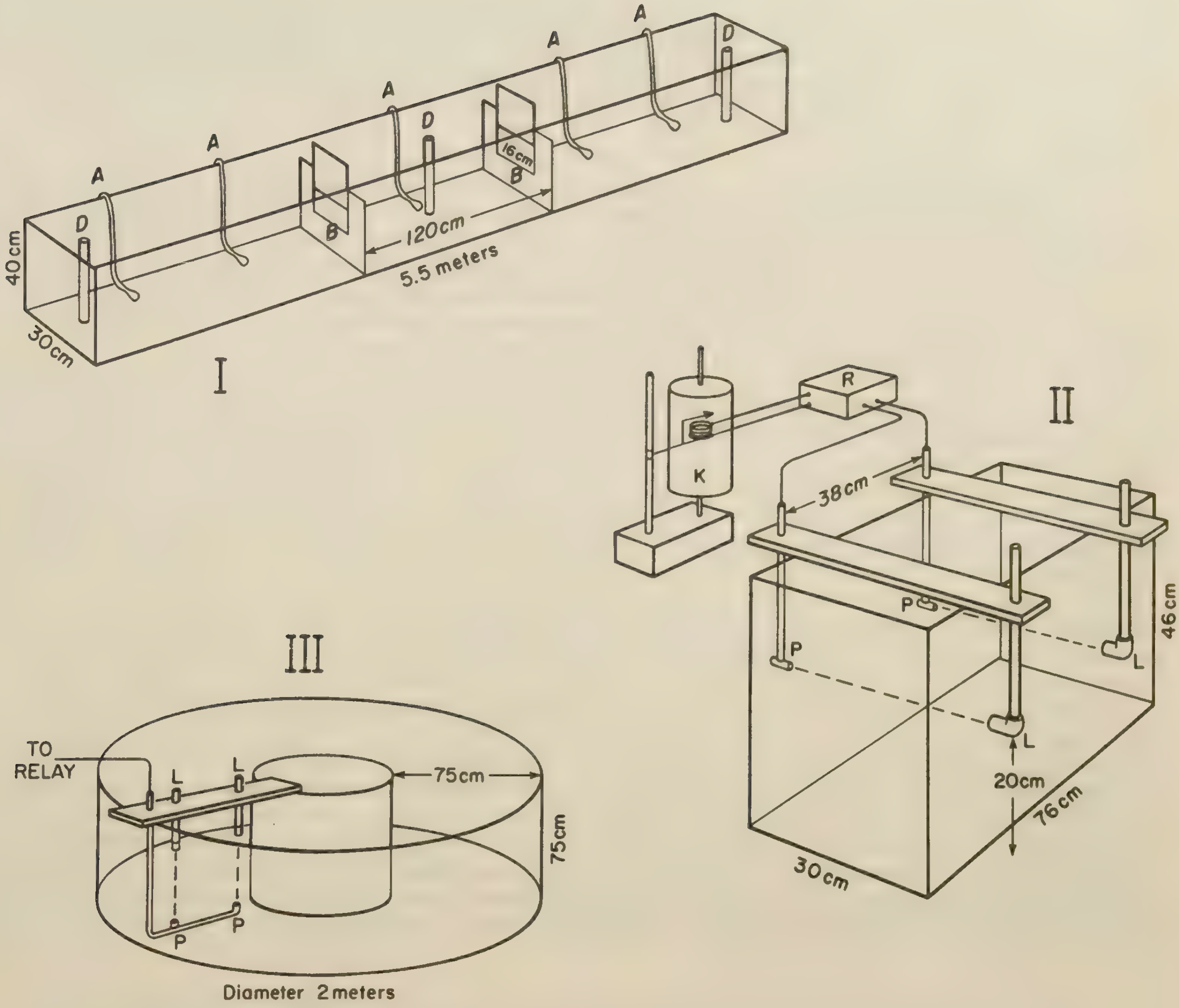
The following experiments were undertaken to determine the responses of herring to variations in temperature and salinity under the relatively controlled conditions of the laboratory.

2 METHODS

Herring used in these experiments, taken from the commercial catches of local fishermen, were 1 and 2 yr old and from 120 to 230 mm in total length when collected. They were held in large, fiberglass-lined tanks at salinities and temperatures which closely followed the seasonal conditions. They were fed regularly on a mixture of canned cat food and dry trout food except during the period of an experiment. when they were not fed because they consistently refused food when out of their "home tank". I therefore tried to limit any experiment to about 1 week, although extension of this period occasionally became necessary. Some deterioration in condition might be expected from fasting, but most of the fish appeared to be healthy and active throughout the experimental period. A few fish died from handling and transfer; weak or moribund fish were removed or replaced before each experiment.

The apparatus used for experiments on temperature and salinity preference was a fiberglass tank, 5.5 m long, 30 cm wide and 40 cm deep. The tank was divided by two transparent panels fitted with sliding doors to form a central compartment and two larger end compartments. Heated sea water or fresh water could be supplied at either end, and excess water drained off through a constant-level drain in each compartment. Five air bubblers provided mixing within the compartments. Stratification, which usually results when an attempt is made to establish a horizontal temperature or salinity gradient in a small space, was virtually eliminated by these bubblers in conjunction with the baffling effect of the two dividing panels. The apparatus is shown in Fig. 1 I.

Each experiment consisted of 4 to 12 trials in which the water at one end of the tank was treated by warming or dilution according to the objective of the experiment. These treatments were reversed end for end with each trial to minimize systemic errors due to any bias of the fish for one end of the tank. Before each trial 10 to 14 herring were held at least 2 h in the center compartment, then released by lifting the sliding doors so that they were free to swim into any part of the tank they chose. Counts were made of the fish in each compartment at 15 min intervals over a period of 2 h.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A
A
A
A
D
D
D
B
B
16cm
120cm
5.5 meters
40cm
30cm
I
R
K
38cm
II
P
P
L
L
46cm
20cm
76cm
30cm
III
TO RELAY
L
L
75cm
75cm
P
P
Diameter 2meters

Fig. 1 Simplified diagrams of apparatus used in experiments (not drawn to scale)

I Temperature and salinity preference tank

A	air bubblers
B	baffles with sliding doors
D	drains

II Small activity tank

K	kymograph
R	relay
P	photo-electric cell
L	light source

III Large activity tank

L	light source
P	photo-electric cell

For statistical analysis, the counts were converted to percentages of the total number of fish employed and averaged for the 2 h period. In a few early experiments, the percentages in warm and cool water were compared for the left side and for the right side of the tank separately. The statistical procedure was a "t"-test; differences between the percentages in cooler and warmer water were considered significant if the "t"-values determined for the left and right sides both exceeded the value for a probability of less than 0.05.

In most of the experiments, however, care was taken to have equal numbers of left-right and right-left arrangements of warm and cool water, and for these a four-way analysis of variance was more satisfactory. The four values compared were mean percentages on the left side when it was the warmer, on the left side when it was the cooler, on the right side when it was the warmer and the right side when it was the cooler. The analysis of variance separated the differences due to temperature from the left or right bias shown by the fish. Salinity preference experiments were similarly analyzed.

The temperature or salinity measurements made at either end of the tank each time the fish were counted were averaged for each experiment. These measurements were taken at the center of each end compartment. All experiments were done under the same lighting conditions : two overhead fluorescent lamps, symmetrically placed with respect to the ends of the tank. Fish were counted by observation in mirrors inclined at 45° above the tank and the observer remained in the room only to make counts and record temperature, salinity or other data.

Adaptation to low and intermediate temperatures preceding the experiments was at the seasonal temperature of the laboratory sea water from which they were taken. Adaptation to high temperature required artificial heating of the water. Fish so adapted were held at 15° about 1 week prior to the experiments, although much shorter periods apparently would have been adequate. Most of the experiments were done in the winter because control of temperature is simpler and more economical by heating than by refrigeration. Temperatures as low as 2°C could be readily achieved without elaborate insulation; I did no work below this temperature. A heat exchanger consisting of stainless-steel coils immersed in a water bath with a 2000-W heater provided the necessary elevation of temperature. A mercury thermoregulator in the warm-water end of the tank gave partial regulation, but irregularities of mixing and variable ambient temperatures caused some variation in the water temperatures over the period of the experiment. This variation is shown in the tabulated data for each experiment.

Tap water served as a diluting medium for salinity experiments. Salinity was entirely under manual control, but continuous readout from a conductivity meter facilitated this control. The possibility of toxic effects from the tap-water plumbing and the stainless steel coils deserved serious consideration, but after a number of preliminary trials I was convinced that any such effect was negligible. The fish showed no ill effects and oriented toward the diluted water as frequently as they did away from it. Free chlorine or the hypochlorite ion appeared not to be a problem and was seldom detectable by orthotolidine tests of the laboratory tap water.

To determine the effect of temperature or salinity on the activity of herring, I used a smaller rectangular tank (Fig.1 II) and a large circular tank (Fig.1 III) throughout which the temperature and salinity were uniform, but in which these characteristics could be modified at will. A battery of photo-electric cells detected interruptions of light beams by the movements of the fish. The number of interruptions per h, recorded on a kymograph, provided a measure of the **activity** of the fish.

Changes in temperature or salinity frequently alter other characteristics of sea water. For example, the concentrations of dissolved gases may decrease at higher temperatures. If the concentrations of the gases are purposely made equal in two water masses of different temperatures, then the degree of saturation must necessarily be different. If the degree of saturation is purposely made equal, as was done in these experiments by aeration, the concentrations must necessarily differ. Thus in presenting a fish with a choice of two water temperatures, one is compelled to offer also a choice of two different dissolved gas levels, either of concentration or of saturation, and the possibility must exist that the fish, apparently responding to temperature. are in fact responding to the differences in dissolved gas. Differing salinities similarly entail difference in pH.

Doudoroff (1938), who studied the effects of some of these concomitant variables on several species of marine fish, found that differences in pH or dissolved gases did not alter the response of the fish to temperature. Because I was working with a different species under a different experimental arrangement, I examined the effect of these variables on herring. Using dissolved oxygen as an index of the amount of dissolved air in the water, I found differences between the warm and cool ends of the tank not exceeding 0.5 part per million. In a separate experiment with temperature held uniform, I added water artificially supersaturated with air under pressure to alternate ends of the tank. Differences equivalent to 0.8 part per million of dissolved oxygen produced no response in the fish. The difference in pH between the highest and lowest salinity used in all experiments was 0.4 pH unit; in any one experiment the difference in pH between the two ends of the tank was so small that it could not be detected colorometrically.

3 DIRECTED RESPONSES OF HERRING TO TEMPERATURE

In the following paragraphs two bracketed sets of mean temperature values are given for each experiment - one pair for the cooler and another pair for the warmer end of the tank. The first value given in each bracketed pair is the mean for all trials where that temperature level occurred on the left hand side of the tank: the second applies similarly to the right hand side. Detailed data are summarized in Table I.

3.1 General behavior of herring in tank

When the fish were released from the center compartment they first swam throughout the tank apparently at random. Within a few minutes, however, a predilection for one end or the other became manifest. Although a predominance in numbers in that end persisted, the individual fish were not always the same; milling about and excursions from one compartment to another took place continuously. No real schooling behavior occurred, although the fish tended to stay in loosely knit groups. No clear reactions of individual fish to temperature differences were apparent: choices seemed to be made gradually by repeated sampling of conditions in various parts of the tank.

3.2 Temperature preferences of herring adapted to low (3°) temperature

When herring adapted to a temperature of 3° were given a choice between cool (2.6 to 2.8°) and warm (5.8 to 5.9°) water, the mean percentages on the cool side were 13 and 17 percent, and on the warm side 59 and 57 percent. When the choice lay in a higher range of temperature, the percentages were 48 and 49 percent on the cool side (5.3 to 5.3°) and 37 and 28 percent on the warm side (10.0 to 9.9°). In both experiments the differences in percentages between cool and warm water were significant : $F = 376$, $P < 0.01$ in the first and $F = 5.68$, $P < 0.05$ in the second.

3.3 Temperature preferences of herring adapted to intermediate (7 to 9°) temperature

When these fish were given a choice between cool (7.5 to 7.2°) and warm (9.8 to 10.2°) water, 26 and 10 percent chose the cool and 64 and 44 percent chose the warm. The differences in percentages between cool and warm water were significant ($t = 6.38$ for the left side, 6.80 for the right; $P < 0.01$).

Table I

Temperature preferences of juvenile herring adapted to various temperature levels

Adaptation temperature (C°)	Side	Mean temperature on cool side (C°)	Mean temperature on warm side (C°)	Mean percentage of fish: On cool side	Mean percentage of fish: On warm side	Number of observations
3°	L	2.6±0.4	5.8±0.2	13	59	72
	R	2.8±0.2	5.9±0.2	17	57	72
	L	5.3±0.6	10.0±0.1	48	37	72
	R	5.3±0.4	9.9±0.6	49	28	72
7–9°	L	7.5±0.5	9.8±0.2	26	64	72
	R	7.2±0.3	10.2±0.3	10	44	72
	L	11.2±0.6	14.2±0.7	65	29	48
	R	11.3±0.5	14.8±0.5	21	6	48
	L	11.0±0.6	13.9±0.5	59	19	42
	R	9.0±0.6	14.8±0.1	42	9	42
	L	14.3±1.7	17.6±1.6	72	2	20
	R	14.9±1.5	17.2±1.4	76	9	20
15°	L	6.8±0.5	9.8±0.3	4	36	36
	R	6.3±0.5	9.7±0.3	3	48	36
	L	8.2±0.6	12.1±0.5	22	2	90
	R	8.5±0.7	11.9±0.5	7	2	90
	L*	8.9±0.4	11.9±0.5	16	35	52
	R*	8.9±0.4	11.7±1.0	22	30	52
	L	11.7±0.5	14.8±0.3	54	56	54
	R	11.5±1.0	14.7±0.3	2	4	54
	L	14.9±0.5	18.7±0.8	76	12	90
	R	14.9±0.5	18.6±0.6	37	1	90

Duration of each trial 2 h except (*) which was 1 h

In a higher temperature range, when the choice was between cool (11.2 to 11.3°) and warm (14.2 to 14.8°) water, 65 and 21 percent chose the cool side and 29 and 6 percent chose the warm. Again the differemce between percentages on the cool and warm sides was significant ($t = 4.17$ and 3.45, $P<0.01$). A second experiment in this temperature range gave similar results.

In a still higher temperature range, cool water (14.3 to 14.9°) was preferred even more strongly to warm (17.6 to 17.2°). On the cool side, the percentages were 72 and 76 percent, but only 2 and 9 percent on the warm side. The differences between percentages on the cool and warm sides were significant ($t = 3.74$ and 3.77, $P<0.01$).

3.4 Temperature preferences of herring adapted to high (15°) temperature

When herring adapted to a temperature of 15° were given a choice between cool (6.8 to 6.3°) and warm (9.8 to 9.7°) water, 4 and 3 percent chose the cool and 36 and 48 percent chose the warm. The differences were significant ($F = 87$, $P<0.01$). At a higher temperature range, 54 and 2 percent chose the cool (11.7 to 11.5°) and 56 and 4 percent the warm (14.8 to 14.7°). A bias toward the left side of the tank was apparent in this experiment, but the differences in percentages between warm and cool water were not significant ($F = 0.19$, $P<0.05$). In the highest temperature range, however, when the choice was between cool (14.9 to 14.9°) and warm (18.7 to 18.6°) water, 76 and 37 percent chose the cool side, but only 12 and 1 percent chose the warm. Preference for cooler water was significant at these higher temperatures ($F = 355$, $P<0.01$).

This series of experiments with fish adapted to 15° left a small gap between 9.8 and 11.5° in the range of experimental temperatures covered. A fourth experiment to cover this gap gave anomalous results. Because the fish showed no preference between 11.5 and 14.8°, and a definite preference between 6.3 and 9.8° for the warmer, they should be expected to show either indifference, or a preference for warmer water in the intervening temperature range. They did neither, but surprisingly seemed to prefer the cooler (8.2 to 8.5°) to the warmer (12.4 to 11.9°) water, behaving in this respect more like fish adapted to a temperature lower than 15°. This result was puzzling, but seemed to indicate that perhaps the fish were becoming re-adapted to a lower temperature during the experimental period. Therefore the experiment was repeated, with the experimental period reduced from 2 h to 1 h. This time the fish showed a significant preference for warmer water : 35 and 30 percent chose the warm (11.9 to 11.7°) water and 16 and 22 percent chose the cool (8.9 to 8.9), $F = 24.5$ and $P = <0.01$.

A very suggestive fact also emerged from this experiment. Two trials were performed each day : one in the morning, preceded by over-night exposure (16 to 18 h) to the adaptation temperature of 15°, and a second in the afternoon. In the intervening time (3 to 4 h) between trials the fish were also held at 15°. The results of the morning trials alone showed an unequivocal preference for warm water : 54 and 28 percent of the fish chose the warm (11.9 to 11.1°) and 6 and 11 percent the cool (8.8 to 8.8) $F = 99.1$ and $P<0.01$. The results of the afternoon trials, however, were erratic and inconclusive. Although a slight preference for cooler water was apparent, it was not significant. It is evident that herring adapted to 15° do prefer the warmer water (as originally inferred) in the 8 to 12° temperature range, and that no real inconsistency exists. It is further evident that a change in behavior occurred after the fish had been exposed to the experimental temperatures. Apparently the experimental temperatures were sufficiently different from the original adaptation temperature for the fish to become partially re-adapted to a lower one.

To what extent the responses of the herring in other experiments were modified by re-adaptation to the experimental temperatures is not clear, but apparently they were not changed enough to create inconsistencies in the results. Perhaps if the experimental temperatures are close enough to the adaptation temperature, the effect of re-adaptation is slight; if, however, the experimental temperatures are widely divergent from the adaptation temperature, the preference is strong enough not to be greatly affected by re-adaptation. Thus only in certain limited ranges of temperature would the effect be noticeable.

The results of the last experiment above shed some light on the duration of exposure required to adapt herring to a certain temperature. Obviously even the relatively brief exposure of 1 h to the experimental temperatures of 8.9° to 11.9° was enough to alter the responses of herring held 1 week previously at 15°, and presumably adapted to that temperature. Moreover, the overnight exposure between experiments, lasting 16 to 18 h was adequate to restore the same responses shown immediately after the original adaptation period of a week. If a week's exposure to some temperature results in responses characteristic of fish fully adapted to that temperature, and a 16 h exposure results in similar responses, then 16 h seems to be adequate to fully adapt the fish. The 4 h interval between morning and afternoon experiments was not sufficient to restore this characteristic response, hence the time required for complete adaptation must be greater than 4 h. Partial adaptation, that is, an exposure to a new temperature sufficient to alter the response characteristic of the original adaptation, apparently takes places in an hour or less.

4 DIRECTED RESPONSES OF HERRING TO SALINITY

4.1 Salinity preferences at low temperature

Herring used in these experiments were adapted to seasonal salinity and temperature conditions : about 32 o/oo and 3 to 5°C. Due to some mixing in the experimental tank when one side was diluted the highest salinity obtainable was 31 o/oo and the average on the high salinity side of the tank was somewhat lower. Preferences between salinities above about 29 o/oo were therefore not determined.

When herring were given a choice between high (28.7 to 29.3 o/oo) and low (25.8 to 25.6 o/oo) salinity at a mean temperature of 7.3°, 58 and 34 percent of them chose the high salinity, 36 and 16 percent, the low. The difference was significant ($F = 71.7$, $P < 0.01$).

Results were similar at a slightly higher mean temperature of 9.2°. When given a choice between high salinity (27.6 to 28.8 o/oo) and low (26.6 to 24.7 o/oo) 48 and 21 percent of the fish chose the high and 35 and 14 percent the low. The difference was significant ($F = 5.83$, $P < 0.05$).

4.2 Salinity preferences at high temperature

The experiments gave conflicting results at temperatures of 14°C or higher. Although slight reductions in salinity seemed to be preferred during the winter, no significant preference at all could be detected in the summer. Given a choice between high (28.2 to 27.9 o/oo) and low (25.9 to 25.7 o/oo) salinity in water artificially warmed to 14.8° in winter, 55 and 41 percent of the herring selected the lower and 40 and 15 percent the higher. In a similar experiment at seasonal temperature during the summer, no significant preference was shown, nor was any preference apparent at lower salinity ranges at any time. The results of the salinity preference experiments are summarized in Table II.

The difference between results in winter and summer could have been due to seasonal changes in the responses of the fish or because during the winter the fish were not adapted to warm water whereas in summer they were.

4.3 Effect of adaptation on salinity preference

A group of herring previously adapted for a week to a salinity of 23 o/oo were given a choice between mean salinities of 28 and 26 o/oo at 6 to 7°C. The percentages in the higher salinity were 43 and 19 percent, and in the lower, 65 and 38 percent. The preference for the lower salinity was significant ($F = 36$, $P < 0.01$). Adaptation to low salinity had reversed the salinity preference at low temperature.

Table II

Salinity preferences of juvenile herring at various temperatures

Side	Mean temperature	Mean high salinity (o/oo) and s.d.	Mean low salinity (o/oo) and s.d.	Mean percentage of fish on high-salinity side	Mean percentage of fish on low-salinity side	Number of observations
L	7.3 (winter)	28.7±1.4	25.8±0.9	58	36	90
R	7.2	29.3±1.1	25.6±1.3	34	16	90
L	9.2 (winter)	27.6±1.9	26.6±1.5	48	25	20
R	9.2	28.8±1.3	24.7±2.1	21	14	20
L	14.8 (winter)	28.2±1.2	25.9±0.8	40	55	90
R	14.8	27.9±0.8	25.7±1.2	15	41	90
L	14.9 (winter)	23.9±1.0	20.9±0.7	54	52	108
R	15.0	24.1±1.0	21.0±0.8	20	17	108
L	15.0 (winter)	19.6±1.0	17.3±0.9	6	10	54
R	15.1	20.3±1.0	16.9±1.2	4	1	54
L	15.5 (summer)	30.3±0.9	27.5±1.0	69	62	64
R	15.7	29.8±1.1	28.5±1.2	8	3	64

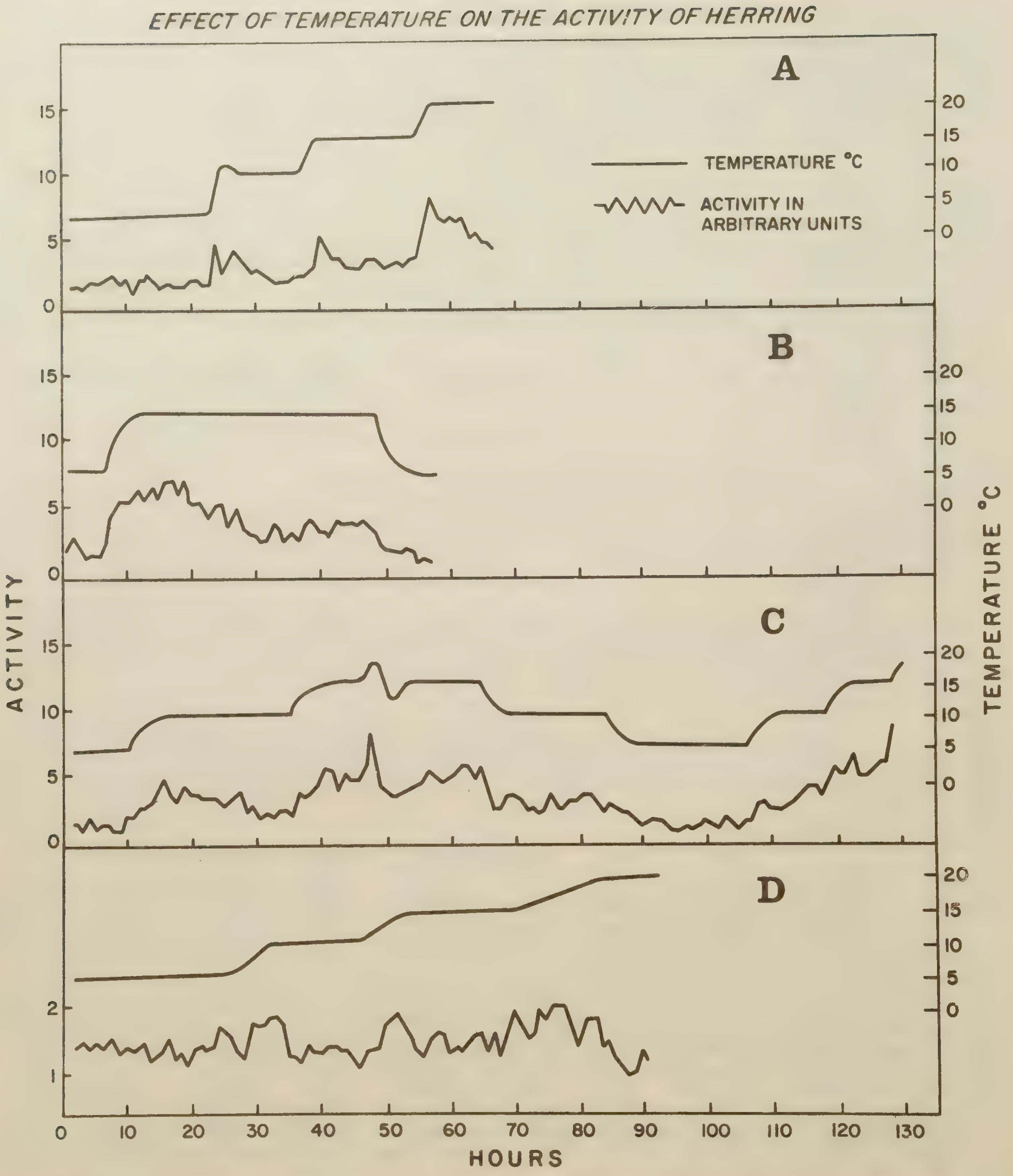

Fig. 2 Effect of temperature changes on the activity of juvenile herring

A	Hourly activity as affected by 5° elevations in temperature
B	Hourly activity as affected by a single 10° elevation in temperature
C	Hourly activity as affected by several elevations and depressions in temperature
D	Hourly activity of herring in uni-directional swimming as affected by 5° elevations in temperature

5 UNDIRECTED RESPONSES OF HERRING TO TEMPERATURE AND SALINITY

Undirected responses, such as changes in activity, could be important in the movements of herring along with those directed responses demonstrated earlier. Several experiments to learn the effects of temperature and salinity on activity were conducted, with the following results:

5.1 General activity of herring

When first transferred to the experimental tank, the herring were highly excited and very active. This initial activity lasted about a day before it declined to a relatively stable level. Irregular short-term fluctuations in activity persisted. Diurnal rhythms, very pronounced in herring exposed to daily changes in illumination, did not occur because all experiments were conducted under constant illumination. Repeated observations of herring under constant conditions of light or darkness showed only irregular fluctuations of activity.

5.2 Effect of successive temperature elevations

Five herring, held for 72 h at 4°C before the experiment, were subjected to periodic temperature elevation in 5° increments; each successively higher temperature was maintained 12 to 18 h. Corresponding changes in activity are shown in Fig. 2A. Units of activity are based on the lowest hourly photocell count taken as unity. With each change in temperature, the activity increased sharply at first but gradually declined. The relative initial rise was greater with increasing temperature.

5.3 Effect of single sustained temperature increase

Four herring were held 24 h at 5° C, after which the temperature was raised to 15° and held at that level 38 h. As before, the temperature elevation was accompanied by an initial rise in activity followed by a gradual decline (Fig. 2B). In both of the preceding experiments the decline leveled off at a higher sustained activity than existed at the lower temperature. The initial peak of activity was higher with a single 10° temperature elevation than with two successive 5° elevations. The sustained activity at 15°C was about the same in both experiments .... that is, about twice the level at 5°C.

5.4 Effect of temperature reductions

In this experiment, the temperature was raised and lowered several times over a longer period of time (Fig.2C). The objective was mainly to determine the response to reductions in temperature. The responses of the fish to temperature elevations were less pronounced than in the preceding experiments, probably because the rates of temperature change were slower. Responses to temperature reductions were simple declines in activity. There was no marked initial change followed by a slow return to some sustained level of activity, such as that which took place on a rising temperature.

5.5 Effect of temperature elevation on linear movement

In the previous three experiments the herring were confined in a relatively small container; the activity consisted of both linear movement and turning. The number of turns was partly determined by the size and shape of the tank. A more natural measurement of activity could be made if the fish were not forced to change direction because of the limits imposed by the tank. When held in a circular tank. herring soon acquire the habit of swimming in one-directional circles, following the circumference of the tank. Although they must make a slight but constant correction to the right or left to follow this path, no pronounced turns or changes in direction are necessary.

The activity of herring swimming in this one-directional fashion was measured in a large circular tank (Fig.1C) by the frequency with which two vertical light beams were interrupted as a group of 16 fish swam past in their circuit of the tank. The temperature was maintained at 5°C for 30 h before the start of the experiment. Observations were then made for 30 h at 5°, 14 h at 10°, 14 h at 15° and 10 h at 20°. Because of the large volume of water to be heated, temperature changes took place much more slowly than in the other experiments; the transition periods ranged from 4 h between 5 and 10° to 14 h between 15 and 20°.

The changes in activity (Fig. 2D) were far less pronounced than in the other experiments, although the peaks of activity occurring at the time of temperature change were apparent. During the periods of constant temperature, the activity of the fish declined, and was only slightly higher at 15° than at 5°. At 20°, after the initial peak, activity dropped markedly to an even lower level than at 5°. Since 20° is near the upper lethal limit for unacclimatized herring, this drop in activity is not surprising. After several hours of exposure to that temperature, the fish ceased swimming around the tank and hovered quietly in one quadrant.

5.6 Effect of salinity on activity

Experiments to determine the effect of salinity changes on activity gave inconsistent results. In one experiment, semidiurnal fluctuations from 17 to 31 o/oo produced no measurable change in activity: in another, similar fluctuations of salinity produced only a very weak response.

6 INTERPRETATION OF EXPERIMENTAL RESULTS

The selection by fish of a particular narrow temperature zone from a wide range of available temperatures is a common phenomenon. The temperature thus selected has been called the preferred temperature and has been described for many species of fish. Doudoroff (1938) and others have pointed out that this preferred temperature could be modified by the previous temperature experience of the fish, and furthermore, that this modification was only transient. When a fish adapted to a certain temperature was exposed to a broad gradient, it occupied a preferred temperature zone, became re-adapted to this new temperature and then selected another preferred temperature zone and so on, until the preference ultimately stabilized at one temperature. This behavior was also noticed by Mantelman (1958) who concluded that the ultimately preferred temperature was a fixed characteristic of a population and that modification of preference by adaptation was not only transient but could take place rather rapidly.

It seems to me that where temperature preference is the guiding factor in the movements of fish, some particular preferred temperature is less relevant than the preference shown between any two temperatures. At any point in its journey, the fish must make the choices which will affect its direction on the basis of the only temperature information available to it at the moment : namely, whether the water it is entering is warmer or colder than that which it was in at some preceding moment. For this reason I believe that presenting the fish with only two temperature choices at a time creates a more natural experimental approach than does presenting them with a broad gradient compressed to dimensions suitable for a laboratory tank. The preferred temperature can be estimated from the choices made. Once determined, the preferred temperature becomes a reference point from which to predict the responses of the fish to any temperature alternatives.

I estimated the preferred temperatures of herring by extrapolation from the preferences shown in the various temperature alternatives offered to the fish. Herring adapted to 15° showed a strong preference of 15° to 18.7° but no preference between 11.5° and 14.8°. From these observations, I inferred a preferred temperature about midway between 11.5° and 14.8°, or about 13°. Herring adapted to 7 to 9° showed a strong preference for 10° over 7° and an equally strong preference of 11° to 14°. This reaction would indicate a preferred temperature of 10 or 11°. Herring adapted to 3° showed a strong preference of 5.3° to 2°, and a weak preference of 5.5° to 10°. Although this choice suggests a preference of about 5°, the weakness of the preference of 5.5° to 10° suggests that the actual preferred temperature lies between 5.5° and 10°, though closer to the lower. I estimated a preferred temperature of 6 or 7°. Although the preferred temperatures calculated in this way can not be precise, a useful set of values can be obtained. A graphic interpretation of the data is shown in Fig. 3.

If the calculated preferred temperatures are plotted against adaptation temperature, a curve is obtained (Fig.4) which is qualitatively similar to those derived for other species, many of which have been assembled from the literature and figured by Ferguson (1958). The point at which the plotted curve intersects the diagonal where adaptation and preferred temperatures are equal is the "final preferendum" of the herring and is that temperature which would ultimately be selected when a complete range of temperatures was available.

Activity of herring increased with temperature; the maximum activity occurred just under the upper lethal temperature. In this respect, the results are somewhat similar to those of Sullivan (1954) who found a peak of activity in trout just below the lethal temperature. Unlike the results of Sullivan, however, the herring showed no indication of maximum activity at the temperature preferendum.

The responses of the herring were of two kinds : a surge or temporary peak of activity accompanying the change in temperature followed by a decline to a relatively steady level somewhat higher than that which occurred at the next lowest temperature. This pattern could be interpreted as two separate responses, one to the change in temperature acting as a stimulus and the second a more general response of the body metabolism to higher temperature; or it could be interpreted as two phases of the same response : the first part that of the fish unacclimated to the new temperature, the second of the fish as it became acclimated to the new temperature.

The weak responses of the steadily swimming fish (Fig. 2D) were undoubtedly due to the much slower changes in temperature, but whether this effect was because the slower change permitted the fish to become acclimatized as the temperature increased, or because the slower change was a weaker stimulus is not evident.

7 ECOLOGICAL SIGNIFICANCE OF TEMPERATURE AND SALINITY PREFERENCE

Interpretation or prediction of herring behavior in the light of the temperature or salinity preferences described here must be made with certain reservations. In the first place, the preferred values may vary according to the age of the herring and the race or population to which they belong. The preceding results and subsequent remarks apply specifically to juvenile Atlantic herring from the Gulf of Maine. Secondly, temperature or salinity preferences may vary seasonally. Such variation has been demonstrated in other fish (Zahn 1963; Sullivan and Fisher 1953).

Little definite information is available about the movements of juvenile herring in the New England and eastern Canadian waters. We do know that from late spring until early fall, they frequent the shallow waters close to land, a habit which makes fixed weirs and stop seines effective fishing gear. During the cold months they apparently disappear from this habitat and move into the deeper waters offshore, where they are taken occasionally throughout the winter by purse seines or trawls, sometimes only a few miles from land. During their summer sojourn inshore they appear in a particular locality for a short time, and then reappear or move on in a rather unpredictable fashion, although they seem to be regular annual visitors to certain localities and may be seen seldom in others. Because hunting for the schools is a major and critical part of the fisherman's work, an understanding of the guiding forces behind the wanderings of these schools could greatly increase the efficiency of the fishery. Temperature and salinity may not be the most important of these guiding forces, but they must certainly play a part in conjunction with others. Although no conclusive evidence from field observations confirms the conclusions

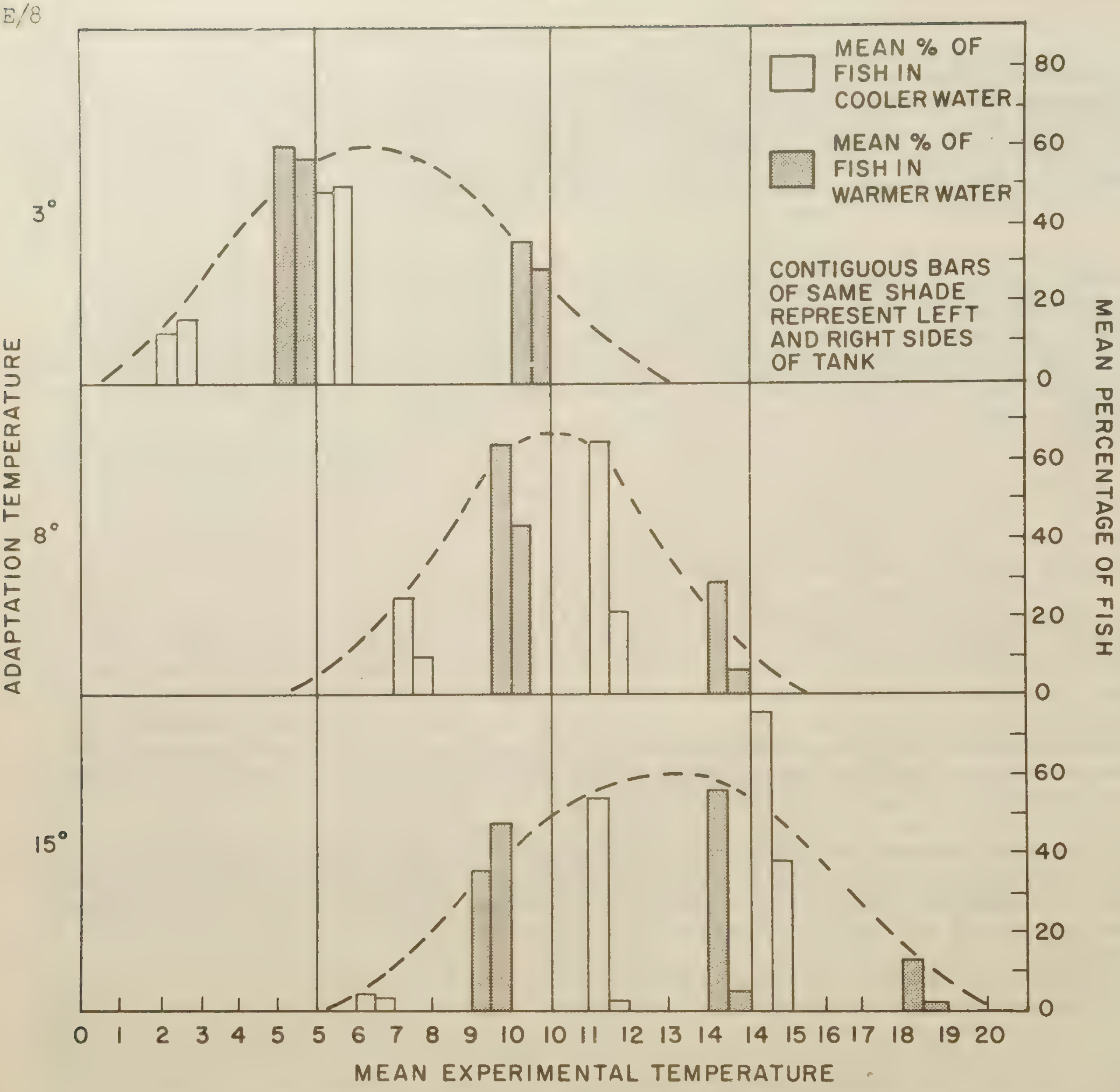

Fig. 3 Temperature preferences of juvenile herring following three different levels of temperature adaptation

Vertical bars = percentage of fish on the cold and warm ends of the tank; left-hand bar of each pair is the percentage on the left-hand side

Dashed line = preferred temperature zone

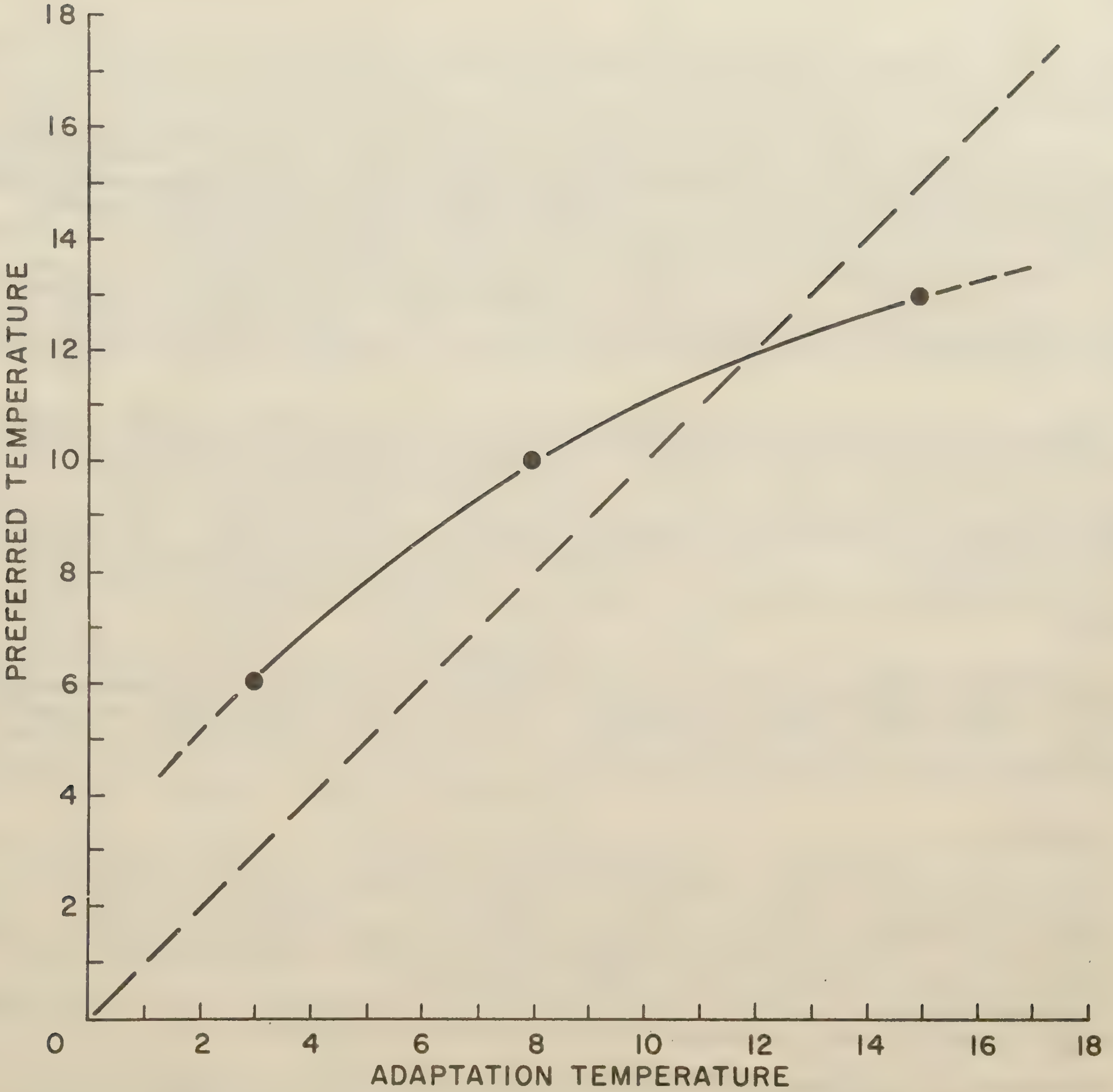

Fig. 4 Relationship between adaptation temperature and preferred temperature of juvenile herring

Dashed line represents locus of adaptation temperature = preferred temperature drawn from the preceding experiments, these conclusions are at least in accord with our limited knowledge of herring behavior.

As cold weather approaches, the shallow, inshore water cools faster and remains slightly colder throughout the winter than the deeper water offshore. At that time, the herring prefer water of a higher temperature than any in their environment; hence the fish would naturally seek the warmest water available: that is move offshore. With the approach of spring, the inshore waters warm soonest and remain warmer throughout the summer. Thus while the temperature is still generally rather low in the spring, the fish still seek the warmest environment and move shoreward. In mid-summer, many inshore areas reach temperatures in excess of 13°C; during that period the herring could be expected to seek the cooler spots, while still avoiding the offshore waters of 12°C or less.

Limited observations of herring movements in the Boothbay Harbor, Maine, area tend to support the hypothesis that herring leave warm areas for cooler ones during the summer. Boothbay Harbor itself frequently reaches temperatures of 17°C or more in mid-summer. The nearby Sheepscot River, however, remains several degrees cooler, and is slightly less saline. Herring appear in the Sheepscot River somewhat later than they do in Boothbay Harbor. A group of 160 herring was tagged in June at Boothbay Harbor; of the 9 recoveries made later in the summer, 6 were from the Sheepscot River and vicinity.

I will not attempt to pursue this argument further, as it is chiefly speculative. The purpose of the discussion is primarily to suggest plausible ways in which temperature and salinity might influence the migration of herring. Heretofore, this kind of discussion would have been pointless because no information was available on the responses of herring to temperature and salinity.

8 SUMMARY

(1) Herring adapted to various temperatures were given choices of warmer and cooler water at several ranges of temperature. Temperature preferences were established from the mean numbers and percentages of the fish that gathered in the warmer or cooler ends of the tank. Similar tests showed salinity preferences at various temperatures.

(2) A final thermal preferendum of about 12°C was estimated.

(3) No final salinity preferendum was established, but at temperatures of less than 10°C it appeared to be greater than 29 o/oo; at 14°C or higher, reactions to salinity were inconsistent and seemed to vary seasonally.

(4) Prior adaptation to different temperatures and salinities produced changes in temperature and salinity preference.

(5) An increase in temperature produced an increase in general activity: an initial peak was followed by a gradual decline to a level somewhat higher than was observed at the preceding temperature.

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ELEMENTARY APPLICATIONS OF SEARCH THEORY TO FISHING TACTICS AS RELATED TO SOME ASPECTS OF FISH BEHAVIOUR

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Abstract

Some aspects of the theory of search are briefly explained and then considered in relation to two general problems concerning fishing tactics. These two problems involve: (a) the proportion of targets (fish or fish schools) entering the effective sighting or capture area under various conditions, and (b) the proportion of targets entering the effective sighting or capture area at various bearings. The latter problem is further restricted to involve a particular search or scanning sector. It is shown that there are certain interesting and potentially useful relationships between the velocity of the observer and the target which are believed to have some bearing on efficient utilization of several types of towed fishing gear as well as for visual or instrumented observations.

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APPLICATIONS ELEMENTAIRES DE LA THEORIE DE LA RECHERCHE AUX TACTIQUES DE PECHE DANS LEURS RAPPORTS AVEC CERTAINS ASPECTS DU COMPORTEMENT DU POISSON

Résumé

Les auteurs exposent brièvement certains aspects de la théorie de la recherche, qu'ils étudient dans leurs rapports avec deux grands rpoblèmes intéresant les tactiques de pêche, à savoir: a) proportion de cibles (poissons ou bancs de poissons) pénétrant dans le champ d'exploration ou de capture dans diverses conditions; b) proportion de cibles pénetrant dans le champ d'exploration ou de capture à divers relèvements. L'étude de ce dernier de recherche ou de balayage. La communication démontre l'existence de relations intéressantes et potentiellement utiles entre la vitesse de déplacement de l'observateur et celle de la cible, qui interviennent probablement tant dans la bonne utilisation de divers types d'engins de pêche remorqués que dans les observation ou faites visuelles au moyen d'instruments.

APLICACIONES ELEMENTALES DE LAS TEORIAS DE LA LOCALIZACION A LAS TACTICAS PESQUERAS EN RELACION CON CIERTOS ASPECTOS DEL COMPORTAMIENTO DE LOS PECES

Extracto

Se explican sumariamente algunos aspectos de la teoría de la localización y a continuación se estudian aquéllos en relación con dos problemas generales de la táctica pesquera. Estos dos problemas incluyen: a) la proporción de blancos (peces o cardúmenes) que penetran en la zona eficaz de captura o de avistamiento en ciertas condiciones; b) la proporción de blancos que penetran en la zona eficaz de captura o de avistamiento en varias direcciones. Ese último problema se concreta, además, a un sector particular de investigación o exploración. Se muestra que existen determinadas relaciones interesantes y potencialmente útiles entre la velocidad del observador y el blanco que se cree que influyen en la utilización eficaz de varios tipos de artes de pesca remolcados así como en las observaciones visuales o con instrumentos.

1 INTRODUCTION

The theory of search is considered to be a branch of the broader field of operations research. The latter topic (operations research) has been defined as a scientific method of providing decision makers with a quantitative basis for decisions regarding the operations under their control. The value of operations research has been adequately described and demonstrated in military as well as in industrial applications. This concept has not yet been applied extensively to fisheries problems in spite of the fact that Beverton and Holt (1957) pointed out the significance of searching and optimum fishing tactics in their exhaustive treatment of population dynamics. Indeed, even the more speculative papers (Alverson and Wilimovsky, 1964; Leeper, 1964) have failed to adequately develop operations research as a part of fisheries activities of the future.

During and after World War II the Antisubmarine Warfare Operations Research Group (USA) developed the general foundations of search theory which involves detection, location and identification of targets as well as allocation of effort for these purposes. A portion of this theory and methodology has been published as a series of papers on effort allocation and the theory of search by Koopman (1953, 1956a,b, 1957) as well as by others (Charnes and Cooper, 1958; Danskin, 1962a,b and de Guenin, 1961). Much of this paper is heavily dependent on the theoretical concepts enunciated by Koopman, and portions of his work and notation are utilized herein with only minor modification. The major justification for our effort lies in a further communication of Koopman's theories and a modest attempt to demonstrate their applicability to some of the problems at hand. Thus the purposes of this presentation are: (a) to briefly review some of the background considered relevant to fishing tactics, and (b) to suggest some simple applications and interpretations which it is hoped will stimulate further interest and developments in search theory, especially as related to the strategy and tactics of fishing.

Some interesting developments and applications of search theoretic concepts have already been made in fishery science. Brock and Riffenburgh (1960) have described a mathematical model of the relationship between fish schooling and predation. Olson (1964) has demonstrated how the results of the Koopman search theory can supplement the inferences made by Brock and Riffenburgh. The kind of information derived from the above mentioned papers is obviously necessary for a better understanding of the theory of fishing and the conservation of fish stocks. It relates to such questions as the probability of a predator locating and/or consuming a given portion of a school of fish based on data or assumptions regarding the distribution, abundance and behaviour of predators and prey. The analogy to fishing operations is obvious.

Some work has also been published in the Soviet Union which is directly applicable toward improved fishing tactics. Of special importance is a paper by Zonov and Gulin (1963) which provides a mathematical background for stationary gear design based on the quantification of some aspects of movement behaviour. Another valuable contribution by Truskanov and Shcherbino (1966) deals with the determination of the density and numerical abundance of herring by means of echo sounding surveys. The possibilities for further application of this work are extremely broad.

In this paper we will restrict ourselves to simple questions involving the location of fishes and the allocation of searching effort to the detection of fish or fish schools, with some notes on the utilization or interpretation of behavioural information related to trawling operations.

2 SWIMMING BEHAVIOUR RELATED TO SEARCH TACTICS - BACKGROUND

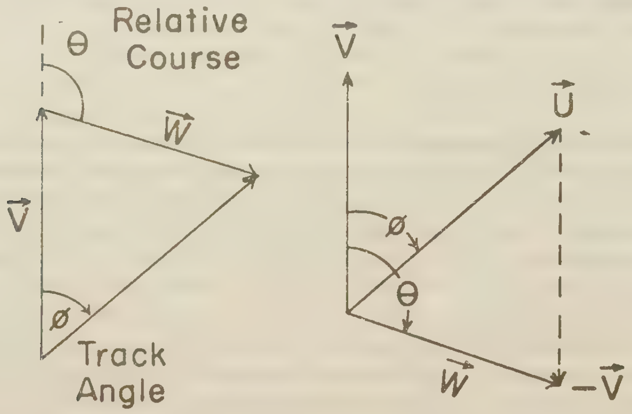
An important but not intuitively obvious problem involves calculation of the proportion of targets (fish or fish schools) which pass within the range of a particular type of search or capturing device as related to the swimming behaviour of the targets (fishes). There are two questions which seem especially relevant to fishing tactics for which answers will be developed.

V = Speed of Observer

U = Speed of Target

W = Speed of Target relative to Observer

$\vec{V}$, $\vec{U}$, and $\vec{W}$ = Vector Velocities


θ
Relative Course
$\vec{W}$
$\vec{V}$
ø
Track Angle
$\vec{V}$
$\vec{U}$
ø
θ
$\vec{W}$
$-\vec{V}$

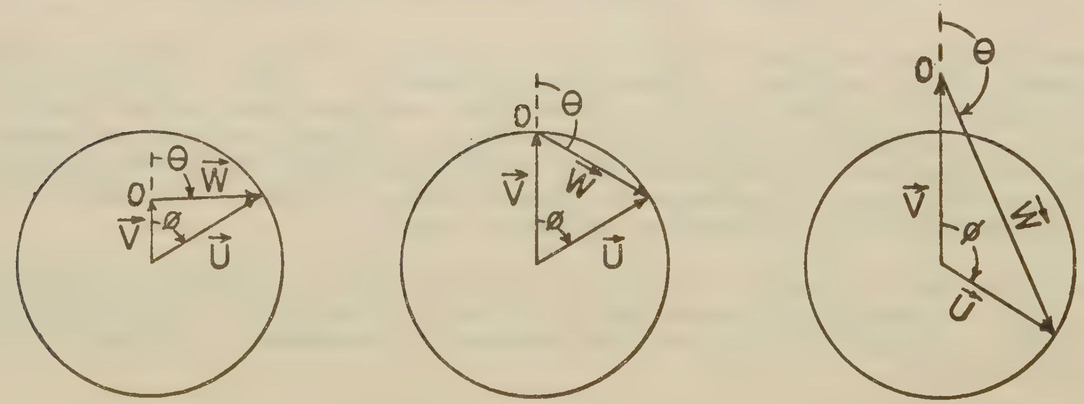
$$\vec{W} = \vec{U} - \vec{V}$$

ø = Angle between $\vec{V}$ and $\vec{U}$ measured clockwise from $\vec{V}$ to $\vec{U}$.

θ = Angle between $\vec{V}$ and $\vec{W}$ measured clockwise from $\vec{V}$ to $\vec{W}$

Angles measured in radians: $0 \leq ø < 2\pi$, $0 \leq \theta < 2\pi$

for $\vec{V} < \vec{U}$, $\vec{V} = \vec{U}$, $\vec{V} > \vec{U}$


θ
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θ
0
$\vec{V}$
ø
$\vec{W}$
$\vec{U}$

Fig. 1 True and relative velocities with angles and circles of relative velocities (after Koopman, 1956a p.325-7)

Before attempting to answer these specific questions it is necessary to introduce some preliminary concepts based on the movement of both the observer and the target at constant speeds in straight lines. The terms observer and target will be used, and these can denote various relationships between a fishing boat, fishing gear and fish, either as groups or individuals. These relations are demonstrated in Fig. 1. With reference to the circle of relative velocities, in each case the radius of the circle around which the extremities of $\vec{u}$ and $\vec{w}$ move is u, and the distance of its centre from the origin O of $\vec{w}$ is v. As ϕ goes from $0 \rightarrow 2\pi$, $\vec{v}$ stays fixed, $\vec{u}$ rotates with its length remaining constant and $\vec{w}$ changes in both length and direction. Note that when $v < u$ all directions of $\vec{w}$ are possible ($0 \leq \theta < 2\pi$), but in the cases ($v \geq u$) this does not hold so that:

when $v = u$, $\pi/2 \leq \theta \leq 3/2\,\pi$;
when $v > u$, $\pi - \sin^{-1}(u/v) \leq \theta \leq \pi + \sin^{-1}(u/v)$.

The above corresponds to the fact that when the searcher is faster than the target, relative approach of the target to the searcher is restricted.

When $v > u$, two values of w correspond to general values of θ for which approach is possible; one for the target approaching the observer, the other for the overtaking of a target heading away from the observer. When $\theta = \pi \pm \sin^{-1}(u/v)$, there is just one value for w; for other θ's there is no value.

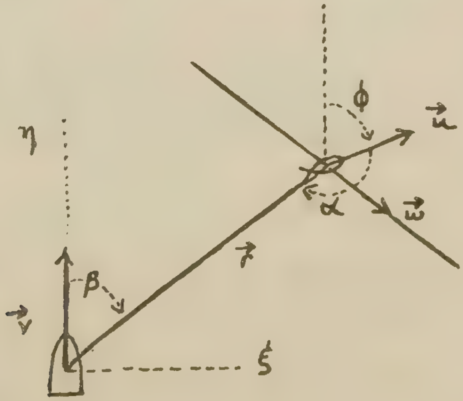
The relative speed w can be found from the law of cosines, or by projecting $\vec{v}$ and $\vec{u}$ on $\vec{w}$ and using the law of sines; similarly for ϕ. This expresses relative quantities in terms of true:

$$w = \sqrt{u^2 + v^2 - 2uv\cos\phi} = -v\cos\theta \pm \sqrt{u^2 - v^2\sin^2\theta},$$
$$\sin\theta = (u/w)\sin\phi.$$

To specify a particular contact between observer and target, we must be able to state the position of the target relative to the observer at any given instant of time (epoch) t. To do this we must have target range r, relative bearing β, and target angle α where:

$\vec{r}$ = vector from observer to target
r = length of $\vec{r}$ in miles
β = angle from $\vec{v}$ to $\vec{r}$ measured clockwise
α = angle from $\vec{u}$ to $-\vec{r}$ measured clockwise

When the roles of target and searcher are interchanged, those of β and α are likewise interchanged, $\vec{r}$ being replaced by $-\vec{r}$. The track of the target relative to the observer is shown below:



where: $r^2 = \xi^2 + \eta^2$, $\xi = r\sin\beta$, $\eta = r\cos\beta$.

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One of the simplest and most important cases of random distribution of targets is that of the uniform distribution of targets of given speed u. It complies with the three following requirements:

1. $p(\phi_1 < \phi < \phi_2) = \frac{\phi_2 - \phi_1}{2\pi}$ when $\phi_1 < \phi_2$

2. The probability that at any chosen epoch the target be in the area A is proportional to A, and hence if the target is known to be in a larger area B containing A, the probability that it be in A is A/B.

3. The event of ϕ being between ϕ_1 and ϕ_2 on the one hand and the event of the target being in A on the other are independent events. If one of them is known to have occurred, the probability of the occurrence of the other is the same as before.

In this case the p.d.f. will (when the target is given to be in B) have the value $p(\phi, r, \beta) = \frac{r}{2\pi B}$. This is because $r\,dr\,d\beta$ is the element of area corresponding to a position of range and bearing between r and r+dr and β and $\beta + d\beta$ respectively.

When an observer is progressing on its course at the constant velocity v among a uniform random distribution of targets of speed u, it is frequently important to know the proportions of targets which pass within a range R of the observer. If a circle of radius R is pictured centred on the observer and moving along with it at velocity v over the ocean two questions relevant to fishing operations may be asked:

(a) What proportion of the targets (fish or fish schools) enter the effective scanning, sighting or capture area?

(b) What proportion of the targets enter at various specified bearings?

3 PROPORTION OF TARGETS ENTERING SEARCH AREA

We shall consider question (a) initially. Let there be an average number N of objects (fish or fish schools) per unit area (square mile, for example). The average number with track angle between ϕ and $\phi + d\phi$ will be $Nd\phi/2\pi$. To find the number of targets N_o which enter the circle in a unit of time we fix our attention on a particular track angle ϕ, compute relative speed w and course 0 and draw a circle of radius R about the observer's position (Fig. 2). Since the target is moving at velocity w with respect to the observer, if it is to enter the circle in a unit of time it must be in the shaded region of the figure between a circle of radius R and relative velocity w from the observer's circle (assuming the observer's circle will be displaced -w in one unit of time). The target must also be in the area bounded by the two tangents 180° apart - one at the angle we are interested in and the other at its reciprocal, both being parallel to w. The area is computed to be 2Rw, and since the average number of targets with track angle between ϕ and $\phi + d\phi$ is $Nd\phi/2\pi$, the number that enter the circle per unit of time that have a particular track angle is $2RwNd\phi/2\pi$. The total number N_o that enter the circle per unit of time is given by:

$$N_o = \frac{2\,RN}{2\pi} \int_0^{2\pi} w\,d\phi \qquad w = \sqrt{u^2 + v^2 - 2uv\cos\phi}$$

$$N_o = \frac{RN}{\pi} \int_0^{2\pi} \sqrt{u^2 + v^2 - 2uv\cos\phi}\;d\phi$$

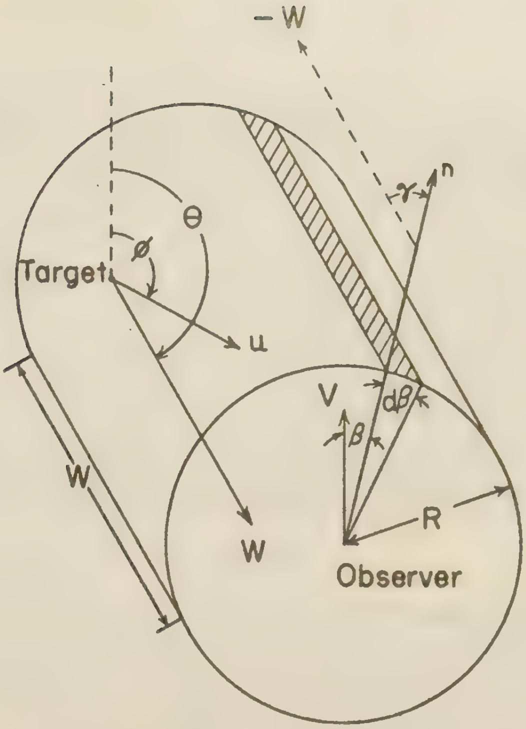
-W
θ
φ
Target
u
n
γ
V
dβ
β
W
W
R
Observer

Fig. 2 Area of targets entering a circle
(after Koopman, 1956a p.335)

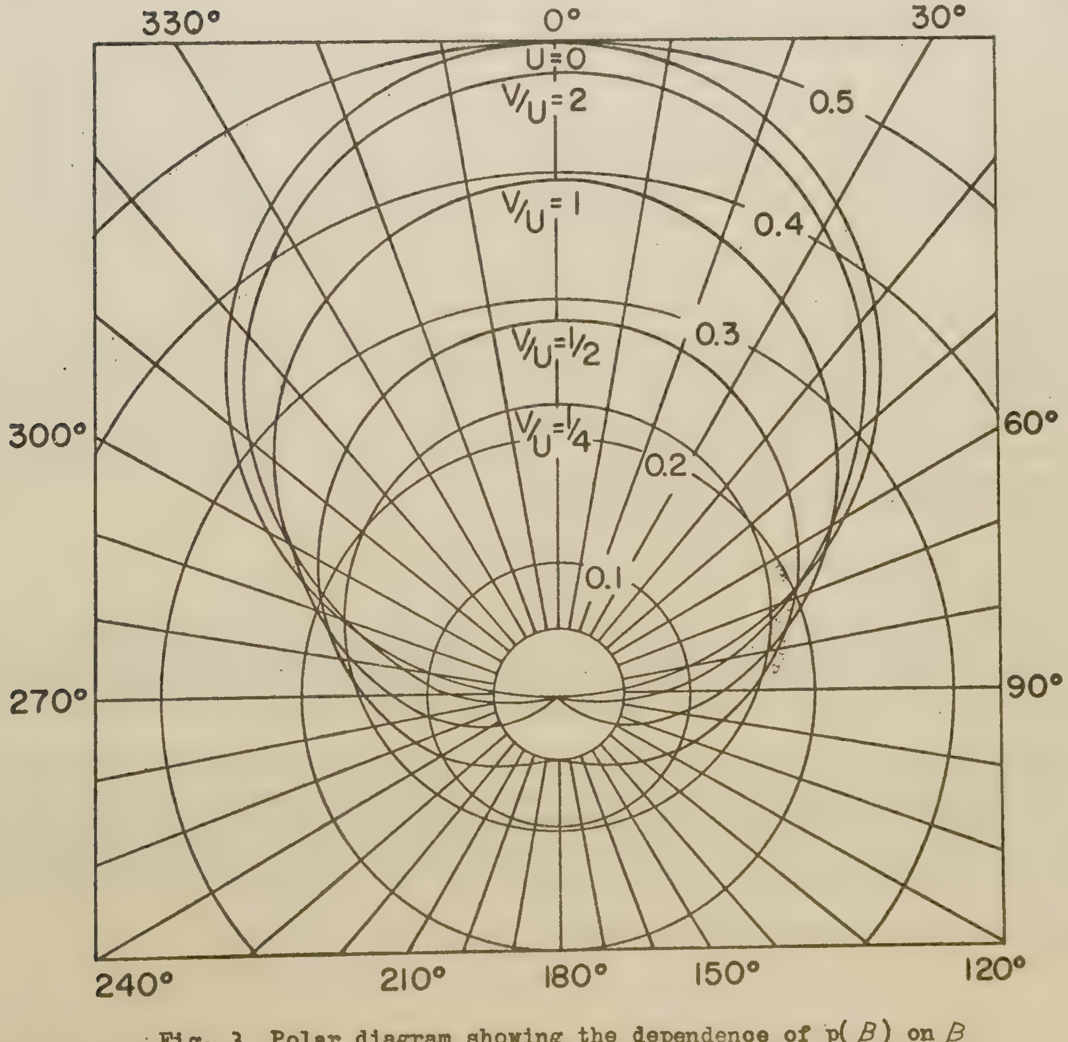

Fig. 3 Polar diagram showing the dependence of $p(\beta)$ on β
(From Koopman 1956a, p.338)

Since symmetry exists:

$$N_0 = \frac{4RN}{\pi} (u+v) \int_0^{\pi/2} \sqrt{1 - \sin^2 \sigma \sin^2 \psi}\, d\psi$$

$$\text{where } \psi = \pi - \phi \qquad \sin \sigma = \frac{2\sqrt{uv}}{u+v}$$

$$\int_0^{\pi/2} \sqrt{1 - \sin^2 \sigma \sin^2 \psi}\, d\psi \Rightarrow \int_0^{\pi/2} \sqrt{1 - K^2 \sin^2 \psi}\, d\psi$$

which is the elliptic integral of the second kind E(σ).

Therefore:

$$N_0 = \frac{4RN}{\pi} (u+v)\, E(\sigma) \qquad (1)$$

Note that equation (1) is left unchanged if u and v are interchanged. This corresponds with the fact that whenever the target comes within range R of the observer, the observer automatically comes within range of the target.

Question (a) Example: Any number of hypothetical examples might be constructed but one will serve to illustrate the utility of the above equation. Suppose there are 100 schools of fish distributed at random in an area of 100 x 100 = 10,000 mi^2. From these data we find that N = 100/10000 = 0.01 schools/mi^2. Assume also that the search vessel is travelling at 5 mph and the fish schools are travelling in various directions at 2.5 mph. The radius of vision of the observer is considered to be 5 mi. We are interested in the number of schools which come within range of the observer per hour. For this example we have: N = 0.01, R = 5.0, u = 2.5 and v = 5. Substituting these values in equation 1 we find that N_0 = 0.54. If now we hold all conditions constant except the speed of the fish schools (which is reduced to 1 mph) and substitute again in equation 1, we find that N_0 = 0.51. The greater magnitude of the first number indicates that the greater speed of movement of the fish bring more of them into the range of the observer than escape from getting within range. This fact is not intuitively apparent and has some interesting applications in fishing tactics. It suggests that if searching effort can be chosen between periods of greater or lesser activity of the fishes then search during the period of greater activity will be the more rewarding. Although the example is hypothetical some of the parameters used are within the limits observed for the tuna fishery. A sighting radius of about 5 mi has been suggested for surfaced tuna schools by McNeely (1961), and Laevastu (1965) has suggested considerably reduced swimming speeds at night.

Interpretation and discussion of question (a):

It seems apparent from the analysis and example that, other factors being fixed, the probability of success in locating fish or fish schools increases with increased movement of the fish. Since u and v are interchangeable in equation 1 the probability of success is also increased with increased searching speed.

The application of search theory related to swimming behaviour may also have implications in the results of trawling experiments and operations. For instance, Bagenal (1958) was unable to explain the significantly higher catches of bottom fish by day than by night in a comparison of the standard trawl and the Vigneron-Dahl modified otter trawl. Others, DeGroot (1964) and Woodhead (1960), also have noted higher trawl catches of plaice by day than by night. From laboratory studies Blaxter and Parrish (1966) have attempted to explain these observations in terms of a decreased directional response to moving netting by night. However, DeGroot (1964) has already suggested another explanation based on stomach analysis and feeding during the day, indicating that plaice activity is greater by day than at night. Based on DeGroot's observation of increased activity during daylight hours our simple illustration of search theory may contribute to an explanation of high day catches inasmuch as the probability of fish moving into the vicinity of the mouth of the trawl is increased by an increase in the amount of movement by the fish. In another context, the improved catches of bottom fish by increased tow speed (Boerema, 1957) may also be partially explained by the fact that equation 1 is unaffected by an interchange of u and v.

The principle illustrated above is that contact rate on random targets increases with increased motion of the targets or increased speed of the search or capturing device. Obviously, there are practical limits to both.

4 PROPORTIONS ENTERING AT VARIOUS BEARINGS

Question (b) involves finding the number of targets which enter the circle between the bearings β and $\beta + d\beta$ per unit time. Their number is given by an expression of the form $N_o(\beta)d\beta$, where $N_o \beta$ is a density related to N_o by the equation:

$$N_o = \int_0^{2\pi} N_o(\beta)\, d\beta$$

To find $N_o(\beta)$, we begin by considering only those targets of a particular track angle ϕ. They can enter the observer's circle only if the direction of the vector $\vec{w}$ points into the circle such that if the angle γ between the reversed vector $-\vec{w}$ and the unit vector $\vec{n}$ normal to the circle and pointing outward is acute (γ is measured between 0 and π). In this case the targets in question all come from the small heavily shaded region of area $Rw \cos\gamma\, d\beta = -R(\vec{w}.\vec{n})d\beta$ where $(-\vec{w}.\vec{n})$ denotes the scalar product (see Fig. 2). The number per unit time is obtained by multiplying this expression by the density $Nd\phi/2\pi$. The number $N_o(\beta)$ for targets of all track angles is given by:

$$N_o(\beta) = \frac{RN}{2\pi} \int (-\vec{w}.\vec{n})\, d\phi$$

where the integration is over all those values of ϕ between 0 and 2π for which the integrand is positive. For the evaluation of the equation we observe that:

$$\vec{w} = \vec{u} - \vec{v}$$

Hence $$-(\vec{u} - \vec{v}).\vec{n} = (\vec{v}.\vec{n} - \vec{u}.\vec{n}) = v\cos\beta - u\cos(\phi - \beta)$$

and $$N_o(\beta) = \frac{RN}{2\pi} \int \left\{ (v\cos\beta - u\cos(\phi - \beta) \right\} d\phi$$

It remains to determine the values of ϕ for which $v\cos\beta - u\cos(\phi - \beta) > 0$. As a result the following expressions are obtained:

$v \leq u$

$$N_o(\beta) = \left(\frac{NR}{\pi}\right) \left\{ v\cos^{-1}\left[-\left(\frac{v}{u}\right)\cos\beta\right] \cos\beta + \sqrt{u^2 - v^2\cos^2\beta} \right\}$$

$v > u$

$$N_o(\beta) = NR\, v\cos\beta \text{ for } -\cos^{-1}(u/v) \leq \beta \leq \cos^{-1}(u/v)$$

$$N_o(\beta) = NR/\pi \left\{ v \cos^{-1}\left[-(v/u)\cos\beta\right]\cos\beta + \sqrt{u^2 - v^2\cos\beta} \right\}$$

for

$$-\cos^{-1}(-u/v) \leq \beta \leq -\cos^{-1}(u/v)$$

or

$$\cos^{-1}(u/v) \leq \beta \leq \cos^{-1}(-u/v)$$

$$N_o(\beta) = 0 \quad \text{for } \beta \leq -\cos^{-1}(u/v) \quad \text{or } \beta \geq \cos^{-1}(-u/v).$$

Now suppose that the target has entered the observer's circle. Where is it likely to have entered? If $p(\beta)d\beta$ is the probability that it entered between the bearings β and $\beta + d\beta$ the expected number $N_c(\beta)d\beta$ which enter per unit time is the number entering per unit time N_o times the probability $p(\beta)\,d\beta$. Thus:

$$p(\beta) = \frac{N_o(\beta)}{N_o} = \frac{\pi N_o(\beta)}{4\,RN\,(u+v)\,E(\sigma)}$$

Figure 3 is a polar diagram showing the dependence of $p(\beta)$ on β for different values of u/v. From the above equation we can see that at one extreme when $u = 0$, $u/v = 0$ and the equation reduces to:

$$p(\beta) = \frac{\pi\cos\beta}{4E(\sigma)}$$

The curve is a circle with the observer at a point on the circumference. At the other extreme $v = 0$, and $u/v = \infty$. In this case the above equation reduces to:

$$p(\beta) = \frac{1}{4E(\sigma)}$$

The targets move but the observer is at rest and the number entering at any particular angle is the same. Thus we have a circle with the observer at the centre. In the intermediate cases as long as $u < v$ there is a certain angular range aft over which no contacts are made. As u becomes greater than v the number of contacts made aft increases rapidly until in the limit as many are made aft as ahead. From what has been described above we know that for $v > u$,

$$N_o(\beta) = NR\,v\cos\beta, \quad \text{for} \quad -\cos^{-1}u/v \leq \beta \leq \cos^{-1}u/v.$$

Also,

$$N_o(\beta) = \frac{NR}{\pi}\left\{ v\cos^{-1}\left[-(v/u)\cos(\beta)\right]\cos\beta + \sqrt{u^2 - v^2\cos^2\beta} \right\}$$

for

$$-\cos^{-1}(-u/v) \leq \beta \leq -\cos^{-1}(u/v),$$

or

$$\cos^{-1}(u/v) \leq \beta \leq \cos^{-1}(-u/v),$$

so that:

$$p(\beta) = \frac{\pi\,v\cos\beta}{(u+v)\,E(\sigma)} \quad \text{for} \quad -\cos^{-1}(u/v) \leq \beta \leq \cos^{-1}(u/v).$$

Therefore:

$$p(\beta) = \frac{v\cos^{-1}\left[-(u/v)\cos\beta\right] + \sqrt{u^2 - v^2\cos\beta}}{4\,(u+v)\,E(\sigma)},$$

for

$$-\cos^{-1}(-u/v) \leq \beta \leq -\cos^{-1}(u/v),$$

or

$$\cos^{-1}(u/v) \leq \beta \leq \cos^{-1}(-u/v).$$

If the observer restricts himself to searching a sector which is in the direction of v then $p(\beta)$ may be optimized by adjusting the observer's speed v if u is known.

Let the area searched be from $-\psi \leq \theta \leq \psi$. If $\psi \leq \cos^{-1}(u/v)$

then $$p(\beta) = \frac{\pi v \cos \beta}{(u + v) E\sigma} \qquad (2)$$

but if $\psi > \cos^{-1}(u/v)$,

then $$p(\beta) = \frac{v \cos^{-1}\left[-(u/v) \cos \beta\right] + \sqrt{u^2 - v^2 \cos^2 \beta}}{4 (u + v) E (\sigma)}, \qquad (3)$$

From this we can see that we may adjust $\cos^{-1}(u/v)$ so that $\psi \leq \cos^{-1}(u/v)$. Therefore we can utilize equation (2) to increase the probability of detecting a target within a defined search sector.

Interpretation and discussion of question (b):

From the above it seems possible to make several suggestions regarding fishing tactics. For example, in the case of visual scanning for fish schools or large surfaced fishes under normal conditions when $v > u$ (boat speed is excess of fish speed) it is clear from Fig. 3 that the target (fish or fish school) is more likely to be sighted on the forward quarter than on either beam. Obviously, if searching or scanning effort must be limited to a portion of the effective search radius then it should be restricted to the forward quarter. This results in relatively little loss in efficiency.

It seems possible to speculate somewhat on the significance of Fig. 3 on trawling operations. Carruthers (1964) has deplored the lack of information on bottom currents since the efficiency of fishing operations could probably be improved with this knowledge. Laevastu (1965) has reviewed the effects of currents on orientation and swimming behaviour and has suggested passive movements with the current under some conditions and normal swimming movement against it under other conditions. Available information suggests that normal orientation is against the current for many bottom species with an effective loss of actual swimming speed. Secondly, the efficiency of the trawl gear is affected by the direction of the tow with reference to the current. It would seem that a careful study of movement behaviour of fishes combined with information on the direction and velocity of currents is a requisite to optimum performance of towed fishing gear. We have demonstrated, on albeit simplifying assumptions, the existence of an optimum ratio of boat speed to target speed if a certain sector of the observer's circle is of prime interest. This situation is analogous to most fishing operations with towed gear.

5 CONCLUSIONS

We have been able to introduce only a small part the theory of search and virtually no mention has been made of effort allocation. There are a number of interesting possibilities for improved fishing tactics and strategy involving the optimum distribution of fishing effort among various fishing areas, and the desirability of continuing fishing operations based on previous knowledge of catch and effort data. These remain to be elucidated further.

However, we suggest that the introduction provided herein demonstrates the high desirability of applying some aspects of search theory to fishing operations especially from the point of view of utilizing the relations between the speed of the observer and the speed of the target for maximizing the probability of successful contacts.

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* * * * * * *

BIG EVENTS ON A SMALL SCALE

by

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Abstract

The behaviour pattern of newly hatched fish larvae until it takes its first meal from the sea is described. Whether the larvae do this by instinct or by learning by trial is discussed in relation to their survival.

LA VIE MOUVEMENTEE D'UNE LARVE

Résumé

L'auteur décrit le comportement des larves de poissons de leur sortie de l'oeuf jusqu'au moment où elles commencent à prendre leur nourriture dans la mer. Il examine, sous l'angle de leur survie, si les larves agissent instinctivement ou manifestent des réactions acquises.

IMPORTANTES HECHOS EN PEQUEÑA ESCALA

Extracto

Se describe el comportamiento de larvas de peces recién incubadas hasta que se alimentan por primera vez en el mar. Se examina, con respecto a su sobrevivencia, si las larvas se alimentan instintivamente o tienen que aprender a hacerlo.

Most marine fishes begin life as minute spherical eggs that drift freely in the sea. In many cases the "shell" of the egg is so transparent that we can easily observe the development from the fertilization of the egg until the larva hatches.

The larva leads a very passive existence during the first week of its life. The large yolk sac it carries makes swimming difficult, and apart from a short excursion now and then it takes life easy for the first few days.

As the yolk sac decreases in size the larva acquires more control over its body, and soon it is swimming quickly but aimlessly about. When the yolk supply is almost exhausted it begins to take an interest in its surroundings. It begins to notice the particles of matter that are floating about in its neighbourhood, the tiny living creatures even smaller than itself and the many particles of debris.

Sometimes it starts to follow one of these specks of life it meets on its way, as if to study this strange apparition it is seeing for the first time, but a moment later it loses interest and takes a new direction in this magic world where everything is new.

When only a bare trace of yolk sac remains the fish larva is no longer content just to look on. It gets into a position of attack, curling its little body into an S-shape as if to put more power behind its strike, but it is only feinting at first.

One day it feels that its apprenticeship is at an end, and it discovers its prey. A tiny crustacean larva is rowing itself laboriously along, towing its clumsy body. The baby fish glides cautiously up. During its training exercise it has discovered that seeing both sides of the matter is often a good idea, so it makes a tour of inspection. Then its body tenses into the usual S-shape and after one lightning movement it swims casually on as if nothing had happened. If we look carefully we shall discover that the nauplius is now in the gullet of the larva.

The larva, no doubt, must have made some calculations, of the distance to its prey, for instance, and of the moment when its jaws had to be opened wide enough that the nauplius would be drawn in easily. This behaviour pattern might well be attributed to inborn instinct. However, it is not always so easy to decide what skills are inherited and what skills are acquired, when we recall how the young fish practised.

Sooner or later two such fish larvae catch sight of one another. Both stop, for mutual inspection. Perhaps both then call it a day but just as often they both feel that further investigation is required and begin a little round dance that ends in both sides taking up a position of attack. The two small S-shapes stare fixedly at each other. Suddenly one of them is gripped by panic and disappears from the scene. The taut S of its opponent slowly relaxes, and it continues its search for something to feed on.

Again one might say instinct, but this time we have two identical fish, in exactly the same situation, with diametrically opposed instincts, that of the coward, and that of the hero.

E/10

All the larvae do not hatch out at the same time, even from eggs fertilized simultaneously. Neither are all of them equally adept. Some of them make no apparent effort at all, they just swim and swim until they meet their inevitable fate. There are others that throw themselves into the thick of things with an insatiable appetite for life. They are always on the move; are always interested in everything. They leave no stone unturned, and an S here and an S there add up to a stomach that is always full. These exceptional individuals can be picked out without difficulty. Between these capable individuals who never miss their aim, and those who never ever make a try there are innumerable degrees of 'fitness for life'.

The egg of the plaice takes about three weeks to hatch, and another two months pass before the larva becomes a recognisable baby flounder. During this time changes take place that transform it from a tiny fish that swims with its back up and its belly down, with one eye on each side of its head, to an absurd looking creature that has both eyes on the top, its body twisted, with the left side now facing down and the right side turned upwards, and a mouth that smiles wryly at the world.

Nevertheless, each little flounder is a masterpiece, and when we sit in front of the aquarium and see thousands of vigorous plaice, each as big as a sixpence, clinging to the glass with their eyes literally standing out of their heads we have to agree with an old fisherman who sat for a long time quietly watching the teeming life of this Lilliputian world. Then he said: "This is almost better than being in church".

* * * * * * *

DISTRIBUTION AND BEHAVIOR OF PACIFIC HAKE AS RELATED TO DESIGN OF FISHING STRATEGY AND HARVEST RATIONALE

by

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Abstract

The results of scientific studies of Pacific hake and how they influenced the development of a new fishery are discussed. This species ranges the eastern Pacific coast from Baja California to Alaska occurring in economically exploitable concentrations off Oregon and Washington during the spring, summer and fall seasons and off southern and Baja California in the winter. The presently exploitable stock is estimated to be between one and two billion pounds with an annual sustainable yield of between 130 and 260 thousand metric tons. A fishing system designed to function effectively in response to the stocks diurnal behavior patterns has been developed and demonstrated. The behavioral aspects of the system design is discussed.

REPARTITION ET COMPORTEMENT DU MERLU DU PACIFIQUE SOUS L'ANGLE DE LA STRATEGIE DE PECHE ET D'UNE EXPLOITATION RATIONNELLE

Résumé

L'auteur examine les résultats d'études scientifiques sur le merlu du Pacifique et la manière dont elles ont influencé la création d'une nouvelle pêcherie. Ce poisson se trouve tout le long de la côte est du Pacifique, de la Basse-Californie à l'Alaska, et en concentrations permettant une exploitation rentable au large de l'Oregon et du Washington au printemps, en été et en automne, et au large de la Californie méridionale et de la Basse-Californie en hiver. On estime que le stock actuellement exploitable se situe entre 500 000 et 1 000 000 tonnes, et peut fournir un rendement annuel soutenu de 130 000 à 260 000 tonnes. Un système de pêche conçu pour donner de bons résultats en s'accordant avec le comportement diurne des stocks a été mis au point et décrit. L'auteur examine les aspects de ce système qui intéressent le comportement.

DISTRIBUCION Y COMPORTAMIENTO DE LA MERLUZA DEL PACIFICO CON RELACION A LA TECNICA DE PESCA Y ESTUDIO RACIONAL DE LAS CAPTURAS

Extracto

Se examinan los resultados de los estudios científicos de la merluza del Pacífico y su efecto en la explotación de nuevas pesquerías. Esta especie se encuentra en la costa oriental del Pacífico desde la Baja California hasta Alaska y se presenta en concentraciones explotables económicamente en aguas de Oregon y Washington durante la primavera, verano y otono, y en aguas del sur de California y de la Baja California en el invierno. Se estima la actual población explotable entre 500.000 y 1.000.000 de toneladas, con un rendimiento sostenible anual entre 130 y 260.000 toneladas métricas. Se ha preparado y demostrado un sistema de pesca proyectado de manera que funcione eficazmente con respecto a las modalidades del comportamiento diurno de las poblaciones. Se exponen los aspectos relativos al funcionamiento del sistema.

1 INTRODUCTION

The Pacific hake (Merluccius productus) has been known to be relatively abundant in waters of the Northeastern Pacific Ocean since the early part of this century. It has been considered by U.S. and Canadian trawl fishermen a "trash" species and trawlers commonly attempted to avoid encountering it during their exploitation of more desirable species.

During the past several years this species has been the subject of investigation by marine biologists of the U.S. and U.S.S.R. The studies represent one of the few instances in the history of fisheries biology where large-scale investments were made to investigate a marine species prior to the establishment of a commercial fishing industry. Pre-fisheries investigations conducted by U.S. and Soviet scientists have included studies of the species' life history, seasonal and bathymetric distribution, abundance, and behavioral patterns. These studies have, since the beginning of commercial fishing in 1966, been augmented by investigation of the biological characteristics of the species (growth and natural mortality rates) and investigation of the feeding habits and patterns.

The rapid acquisition of scientific information in the pre-fishery state and during the early phase of commercial fishing has provided a rare opportunity for fisheries scientists to recommend fisheries strategy, and to propose harvest levels and fishing patterns that could establish a satisfactory fishing rationale.

It is the purpose of this paper to provide information on some aspects of the observed distribution, behavior, and general biological characteristics of the Pacific hake and to subsequently consider these factors in light of establishing an optimum extraction strategy within the framework of a suitable harvest rationale.

It is perhaps appropriate to provide some operational definitions of the key terms employed in this paper. The term "distribution" implies the broad-scale geographic and bathymetric areas of ocean occupancy. "Behavior", by contrast is defined as diel or seasonal patterns of aggregation or distribution of individuals that are the result of reactions to changing features within the environment (stimuli). "Fishing strategy" is used to suggest the development of procedures and choice or development of fishing gear that allow for extraction at a minimum cost and the term "harvest rationale" is used to imply a management concept designed to achieve a maximum sustainable physical yield.

Two sources of information have been used in developing this paper: (1) Published scientific literature and (2) informal and unpublished manuscripts which have resulted from explorations conducted by U.S. or Soviet scientists. I will also take the liberty of making some suggestive remarks concerning fishing strategy and harvest rationale which are a product of personal discussions with my laboratory associates and other U.S. or Soviet scientists.

2 GENERAL BIOLOGY

Pacific hake is often classified as a demersal species, but its distribution and behavior pattern suggest that it, for the most part, leads a pelagic existence, but is often found near the seabed over the Continental Shelf. It feeds almost exclusively on a variety of pelagic fishes or animal plankton and inhabits both oceanic and neritic areas. It is a relatively fast growing species, particularly during the first three to four years and attains maturity at about age three (Fig. 1). Although it apparently undertakes rather extensive migrations, it does not appear to be a highly viable or mobile species as regards its activities within a short time period.

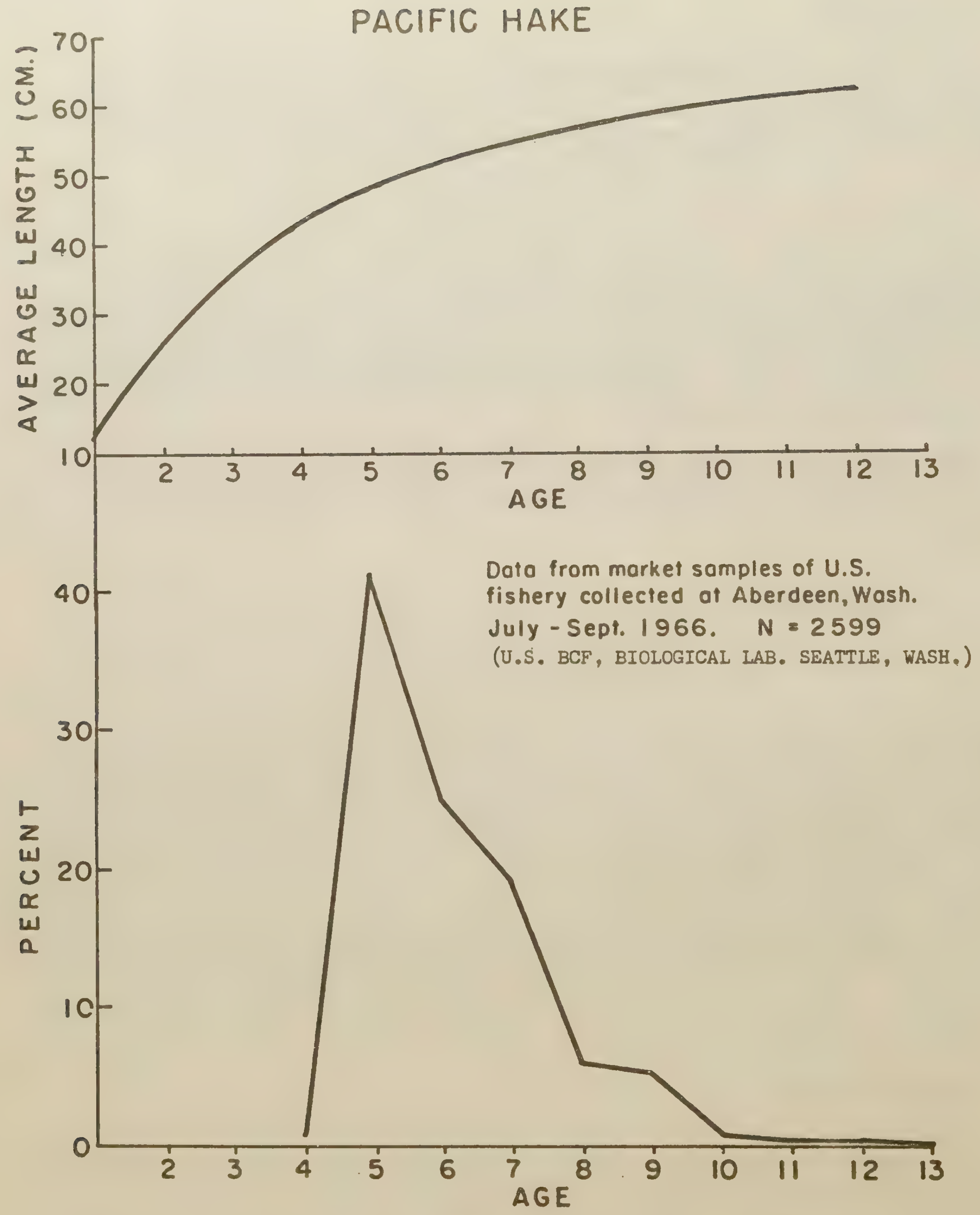


Fig. 1 Age-length and age composition of Pacific hake (Merluccius productus).

3 DISTRIBUTION

Pacific hake, one of the several species of the family Merlucciidae which is harvested commercially from Pacific Ocean waters, has been reported from the Gulf of Alaska (Alverson, Pruter and Ronhalt, 1964) to the Gulf of California (Starks and Morris, 1907). Although this range represents our current knowledge of the species' zoogeographic distribution, commercial concentrations or large accumulations of this species appear to be limited between Baja California, Mexico, and Vancouver Island, British Columbia (Fig. 2). Occurrence of Pacific hake in bottom and midwater trawls suggests that the species inhabits depths from near the surface to at least 800 m (Clemens and Wilby, 1961), and Alverson, Pruter and Ronhalt (1964) note that it is only occasionally taken at depths exceeding 600 m. Commercial concentrations or large accumulations of Pacific hake are known from depths between 50 and 500 m. The mature adult population is normally confined to waters overlying the Continental Slope and Shelf except during the spawning season when they may be found several hundred miles seaward.

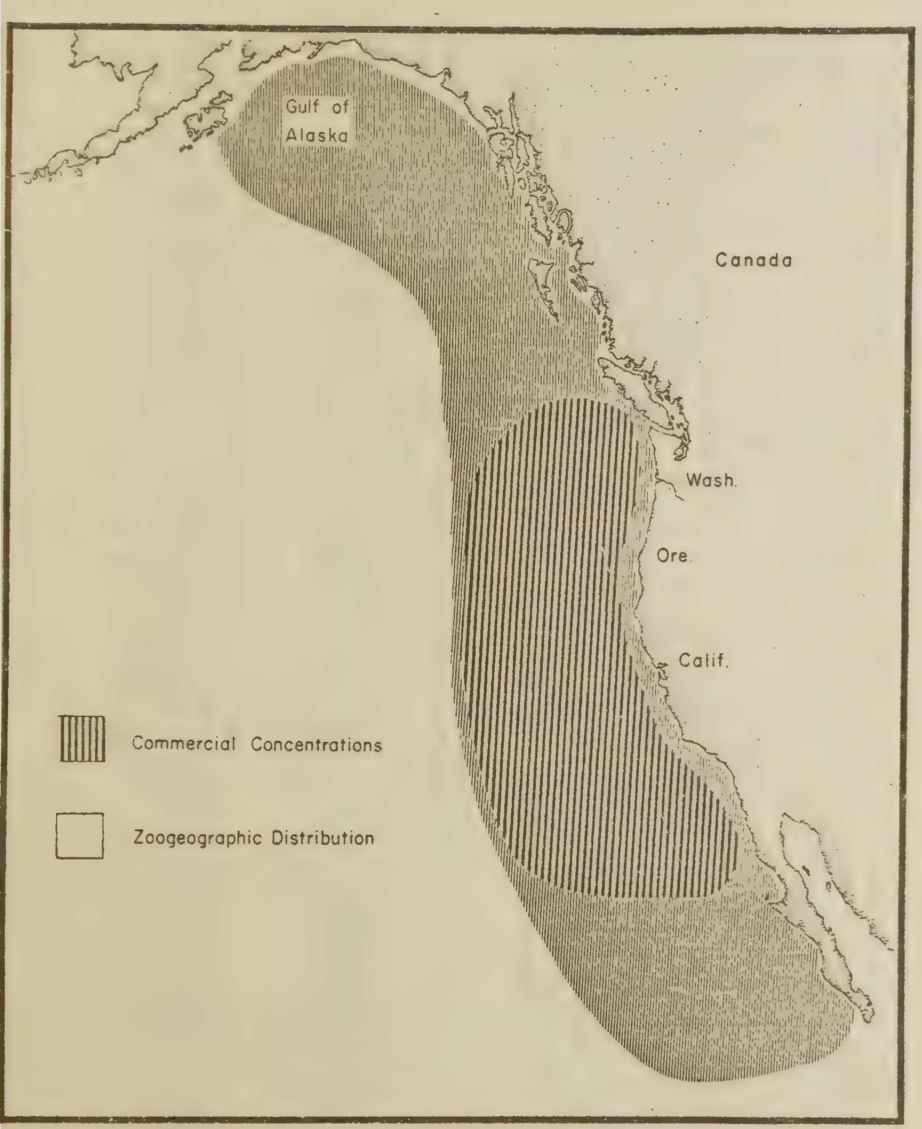
Investigations conducted by U.S. Bureau of Commercial Fisheries and Soviet scientists indicate that the adult portion of the stock occupies the northern portion of the species' range; that is, northern California, Oregon, Washington, and British Columbia during the spring, summer and fall and the southern portion of the range (southern California and Baja California) during the winter. These investigations have demonstrated that the availability of Pacific hake (to bottom and midwater trawls) off Oregon, Washington, and Vancouver Island drops sharply in the month of November and in the winter months is almost completely absent in these waters. During late April and May, hake again become available in the northern part of the range, its availability increasing sharply during the early spring months. The adult stock remains in these areas until late fall.

In the waters adjacent to southern and Baja California, spawning hake have been taken in large quantities during the winter months in offshore waters by the research vessel John N. Cobb. During the period of spawning, the mature stock is concentrated in the deeper portion of its overall bathymetric range (200 - 500 m) and for the remainder of the year (May through November) is found concentrated in waters overlying the Continental shelf at depths less than 200 m.

Ahlstrom and Counts (1955) provide the best usable data on the general bathymetric distribution of eggs and larvae and hence distribution of adult spawning stock. Eggs and larvae of the Pacific hake are reported to occur in large numbers off the coast off southern and Baja California during the winter and late spring months (February through April) with greatest concentrations reported in the waters between Santa Barbara and central Baja California. The eggs and larvae have been encountered in relatively large numbers several hundred miles seaward but highest concentration levels have occurred generally within 200 miles of the coast.

Catches taken during exploratory surveys conducted in the waters between Vancouver Island, B.C., and Baja California have shown a cline in average size of hake taken in various portions of this range. That is, data suggest that during the summer months the average size of hake decreases as one proceeds from north to south. This cline appears to be associated with increased availability of juveniles in the southern extremity of the range and an almost complete absence of juveniles in the more northern waters off Washington and British Columbia.

Investigations of the seasonal and annual distribution patterns and abundance of Pacific hake allow us to propose the following hypothesis concerning the general dynamics of hake migrations: (1) Within the geographic range occupied by Pacific hake, a large-scale north-south movement exhibited by the adult segment of the population. (2) The movement is to the north during the spring and summer and to the south


Gulf of Alaska
Canada
Wash.
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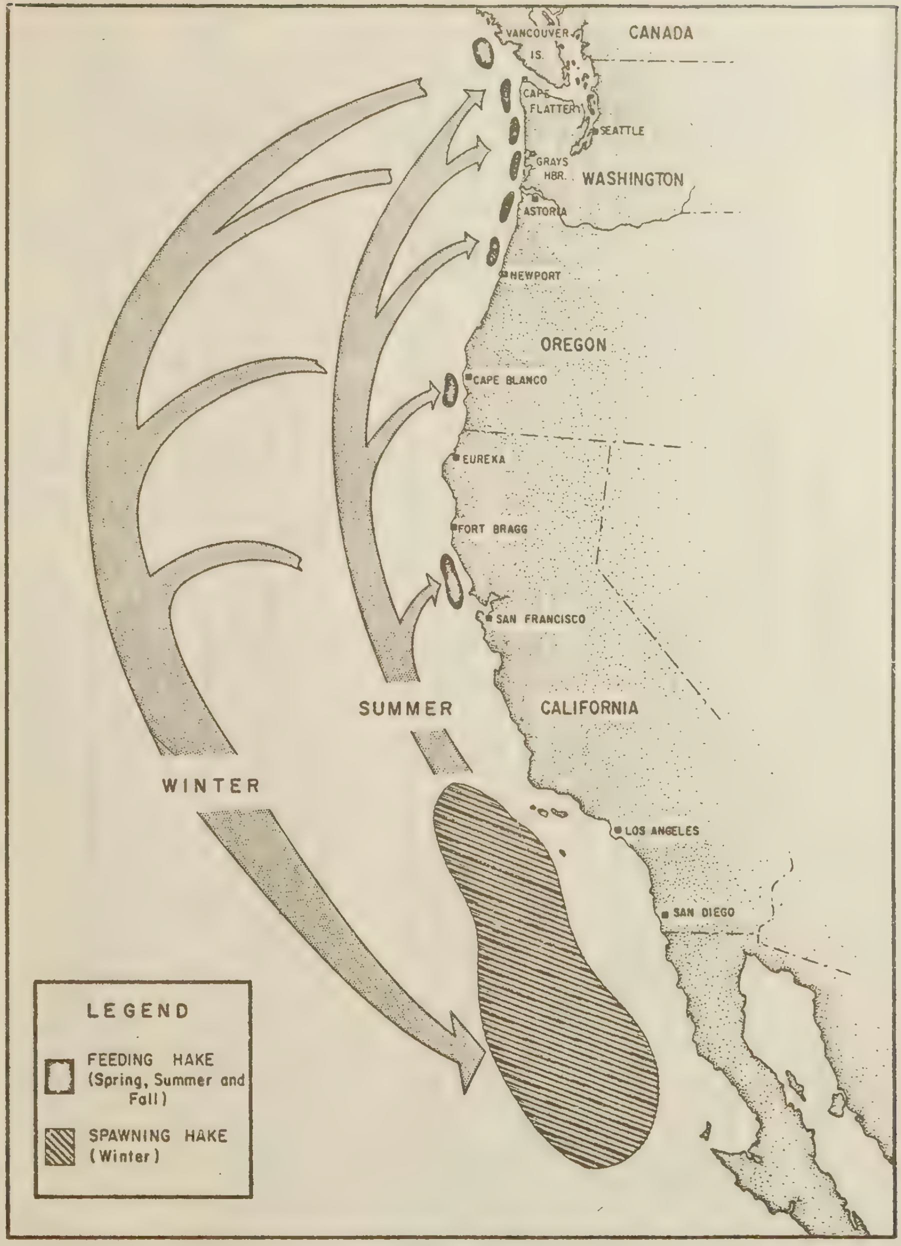
Calif.
Commercial Concentrations
Zoogeographic Distribution

Fig. 2 Zoogeographic distribution of Pacific hake (Merluccius productus) showing area of commercial concentrations.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EUREKA
FORT BRAGG
SAN FRANCISCO
CALIFORNIA
LOS ANGELES
SAN DIEGO
SUMMER
WINTER
LEGEND
FEEDING HAKE (Spring, Summer and Fall)
SPAWNING HAKE (Winter)

Fig. 3 Annual migrations and distribution of Pacific hake (Merluccius productus).

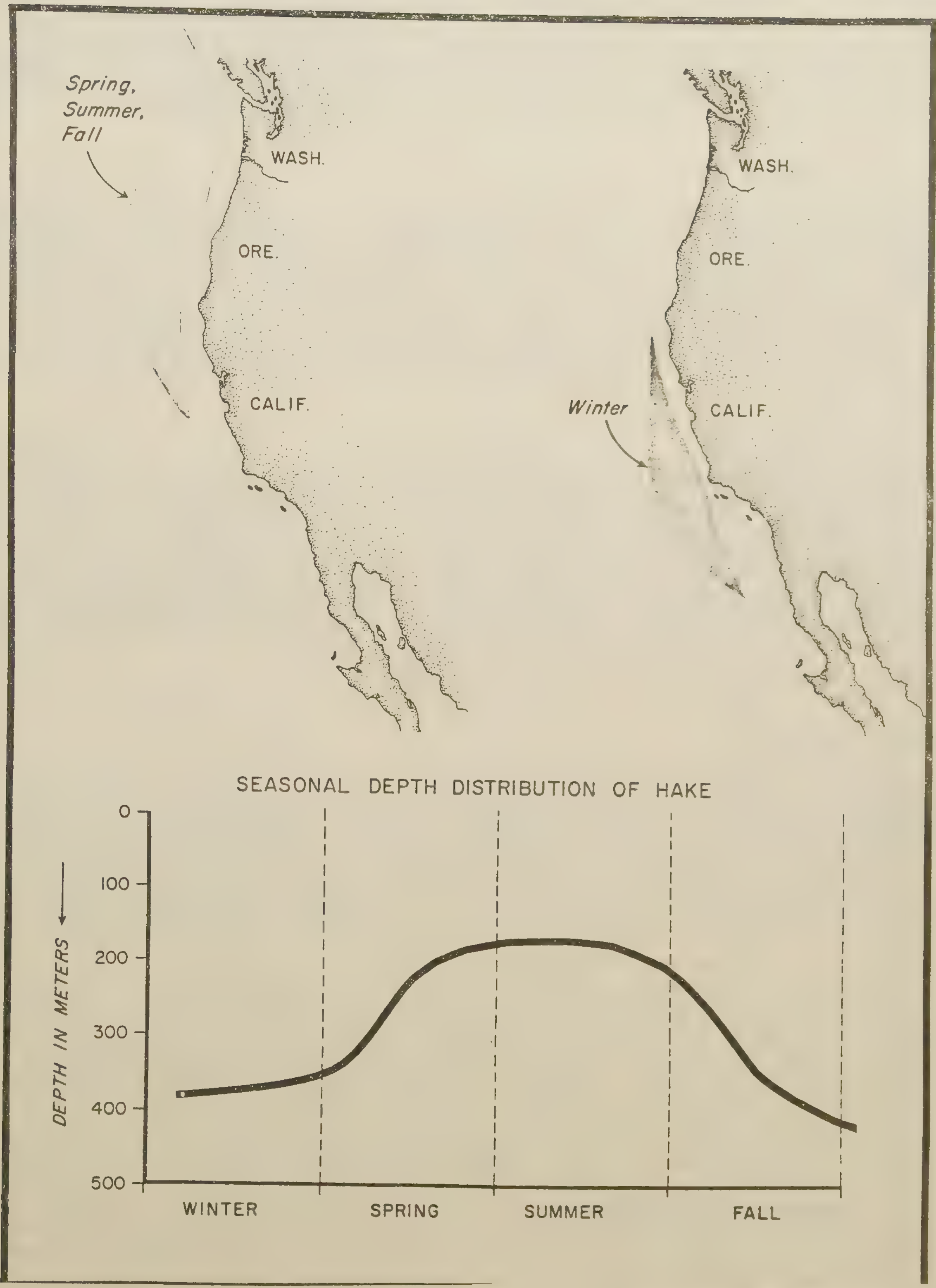

Fig. 4 Seasonal depth distribution of Pacific hake (Merluccius productus) related to geographic area.

during the late winter and fall. (3) The northward migration of the adult stock is accompanied by a movement into shallower segments of the adult bathymetric range and shoreward. (4) The southward migration is accompanied by a movement into deeper water and seaward. (5) Spawning occurs during the winter months when the species occupies the southern portion of its geographic range. (6) The young of the species are recruited to the Shelf but apparently do not enter into the large-scale geographic migrations demonstrated by the adult portion of the stock (Figs.3 and 4).

4 SIZE OF MATURE STOCK

The range of standing stock inhabiting the waters off Oregon and Washington has been estimated by both U.S. and Soviet scientists at between 1 and 2 billion pounds and the forecasted sustainable yield for this stock between 130 and 260 thousand metric tons. It is not the purpose here to explore the assumptions and mathematical models used in forecasting these yields but only to provide you with some concept of the magnitude of the resources. It should be noted that some portion of the mature stock of hake inhabits the waters off California and Vancouver Island so that the total mature stock size would be considerably larger than the figure given above.

5 STOCK COMPONENTS

There are insufficient data available to indicate whether or not segments of the hake population occupying the northeastern Pacific are isolated in a genetic sense. The suggested migration pattern and egg and larva distribution indicate a rather large homogeneous offshore population. This, however, does not preclude the possibility that after spawning, segments of the adult stock colonize specific regions of the Continental Shelf. There is good evidence that the Pacific hake which inhabits the inside waters of Puget Sound and perhaps the Strait of Georgia are a separate stock or population from those inhabiting offshore waters. The growth rate of the Puget Sound stock is substantially slower than for offshore stock.

6 GENERAL BEHAVIOR

During the period that the mature stock inhabits the water overlying the Continental Shelf and Slope, Pacific hake form (Nelson, 1967) schools which may be characterized as long, narrow bands. The axis of these schools are usually oriented parallel to the isobath. Exceptions to this generality are the schools occurring near the continental break (approximately 180 m). At times these schools lie normal to the depth contours extending in an offshore direction. In such instances the inner segment or population of the school will be closer to the seabed than the outer portion of the school. That is, the school maintains the same approximate depth in the water column but its orientation to the depth contours is such that the distance from the seabed to the bottom of the school is continually increasing. The schools may vary in length from several hundred m to 20 km. In most instances, as previously noted, the schools are relatively narrow bands ranging from 0.5 to 0.3 km in width but at times the width of the schools has reached 12 km. In a vertical sense, most of the schools have depths from 6 to 20 m. During the daylight hours these schools lie just off the seabed and at times the bottom of the school is in contact with the bottom. When the schools lie above the seabed, the lower portion of the school can range from 2 to 20 m above the ocean floor. The distance that the schools rise above the seabed varies throughout the day and within the season. For the most part these schools form on the Continental Shelf at depths between 35 and 200 m with the greatest number of schools or concentrations encountered at depths between 50 and 150 m. The schools may persist for several days or disperse within several hours after they have been detected only to re-form several hours later.

In a vertical sense, during daylight hours, the schools seem to be confined to a relatively narrow bathymetric zone and all within the same general depth strata. At times the schools have a relatively constant density pattern and at other times a high degree of density heterogeneity is observed and the overall schools may be composed of a series of clusters or patches (Fig. 5). We do not, however, have any evidence that the hake form vertical feather-like schools such as those that have been observed for the herring fishes.

During the period that the adult population occupies the Continental Shelf, the schools characteristically rise and disperse in the water column during the evening hours. This tendency for hake schools to migrate toward the surface during the hours of darkness has been confirmed by acoustical studies and experimental fishing. Echo studies suggest that the movement begins between 1800 and 2100 hours and by 2300 hours the schools lose their integrity. Data from experimental fishing imply a general scattering of the fish throughout the water column during the hours of darkness. By dawn the fish descend and begin to reform into schools near the seabed. In a geographic sense these schools do not necessarily re-form in the exact area where they were detected on the previous day, but in the same general region.

Studies made in Port Susan, Puget Sound, and off southern California during the spawning season suggest that the behavior of these schools differs from those occuping the offshore shelf waters. Observations of hake schools spawning within Puget Sound suggest one large continuous body of fish which increases in density toward the center of the apparent spawning area (Fig. 6). These schools may be as much as 40 m thick in a vertical plane. The typical daytime trace of spawning hake in Puget Sound shows several characteristic differences from those observed in offshore waters. Aside from the differences in vertical thickness of the schools, the most prominent difference concerns the composition of the traces; that is, those from Port Susan suggest the spawning fish are densely and uniformly spaced within the school.

Although spawning schools of Pacific hake in Port Susan tend to become more scattered as darkness approaches, pronounced vertical dispersal has not been observed. Results of surveys off southern California indicate that the spawning hake populations do not engage in vertical movements of the same nature as those observed on the Continental Shelf. Although there is some apparent movement of nearly ripe fish, most of this diel migration occurs at depths between 180 and 400 m and no fish appear to migrate to waters above the thermocline. Similar to spawning schools in Puget Sound, the adult winter hake population in California appear to congregate in schools of uniform density, but density levels did not appear to be as high as those observed in Puget Sound. It should be noted that in the California area this vertical migration is occurring in the oceanic province where seabed depths are at times greater than 2,000 m.

The diel movement patterns of Pacific hake, fluctuations in depths at which schools are found off bottom, and the relative compactness and size of schools are complex inter-related phenomena that significantly affect the conduct and success of fishing. The reasons for these behavioral patterns are perhaps not as important to fishing success as defining where and when they occur, but in a predictive sense, why they occur could be of future value in planning fishing operations. Alton and Nelson (in press) state the degree to which hake are found congregated or in schools during the day and their subsequent dispersal at night relates to feeding habits and patterns of the species. In the northern portion of the geographic range the adult hake appear to feed extensively on two species of euphausiids, Thysanoessa spinifera and Euphausia pacifica. High catch rates taken by commercial vessels appear to be associated with hake that are feeding almost exclusively on the euphausiid populations, and the lower catch rates occur at such time as the species has a more indiscriminate feeding pattern.

On the Continental Shelf Thysanoessa spinifera has been the dominant euphausiid observed in stomach samples of hake taken off the Oregon-Washington coast. Investigations

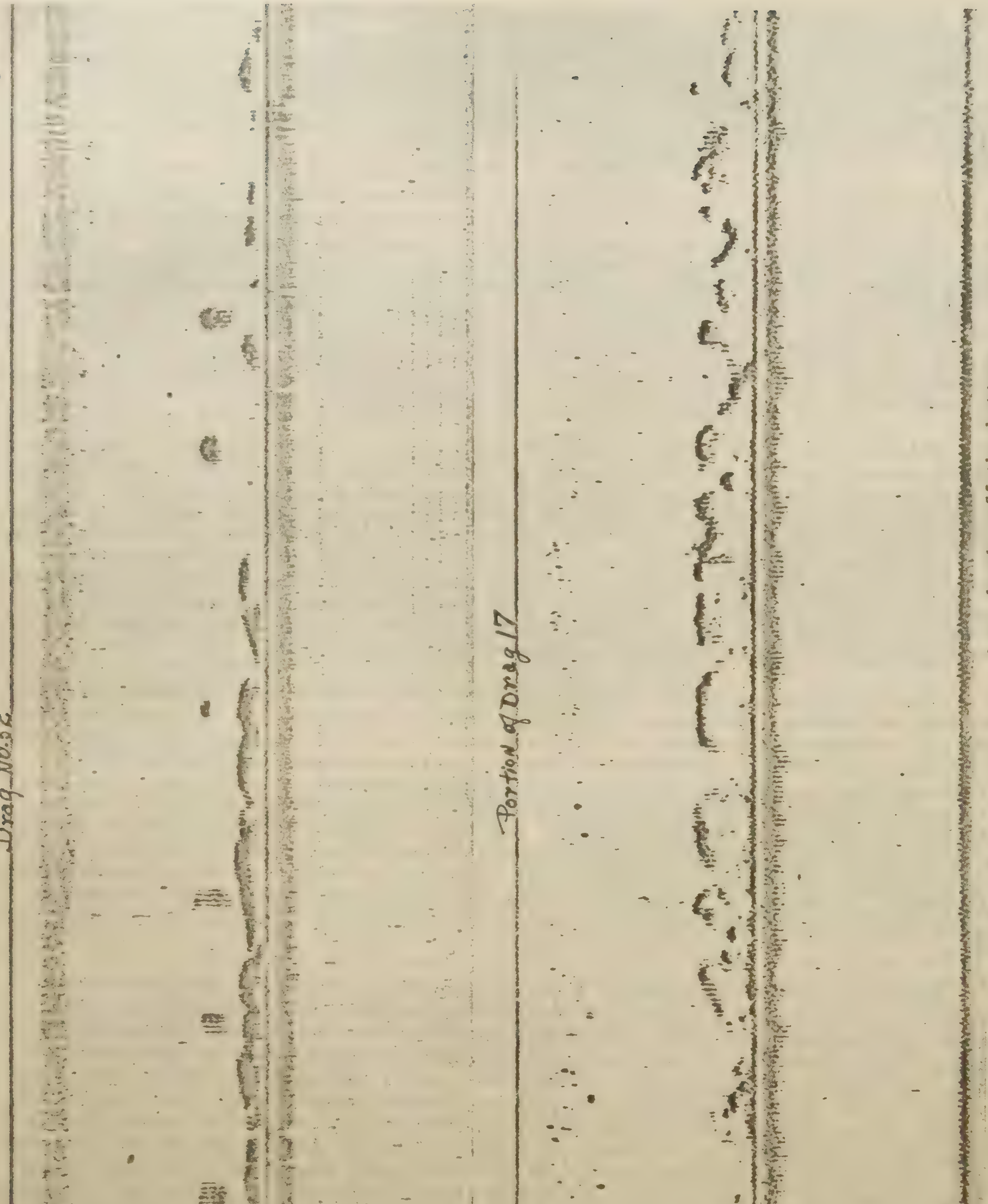

Fig. 5 Echogram showing hake at various depths off the bottom.

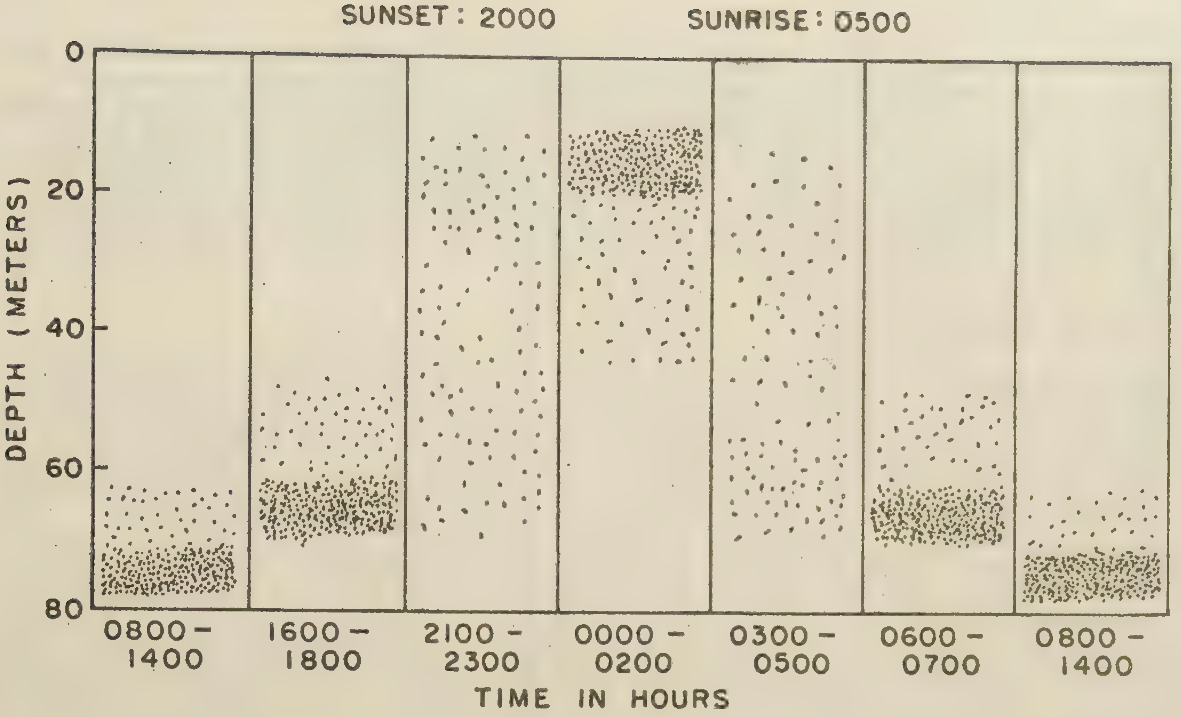

Fig. 7 Diagram showing diel movement of the euphausiid (Thysanoessa spinifera) off the Washington coast.

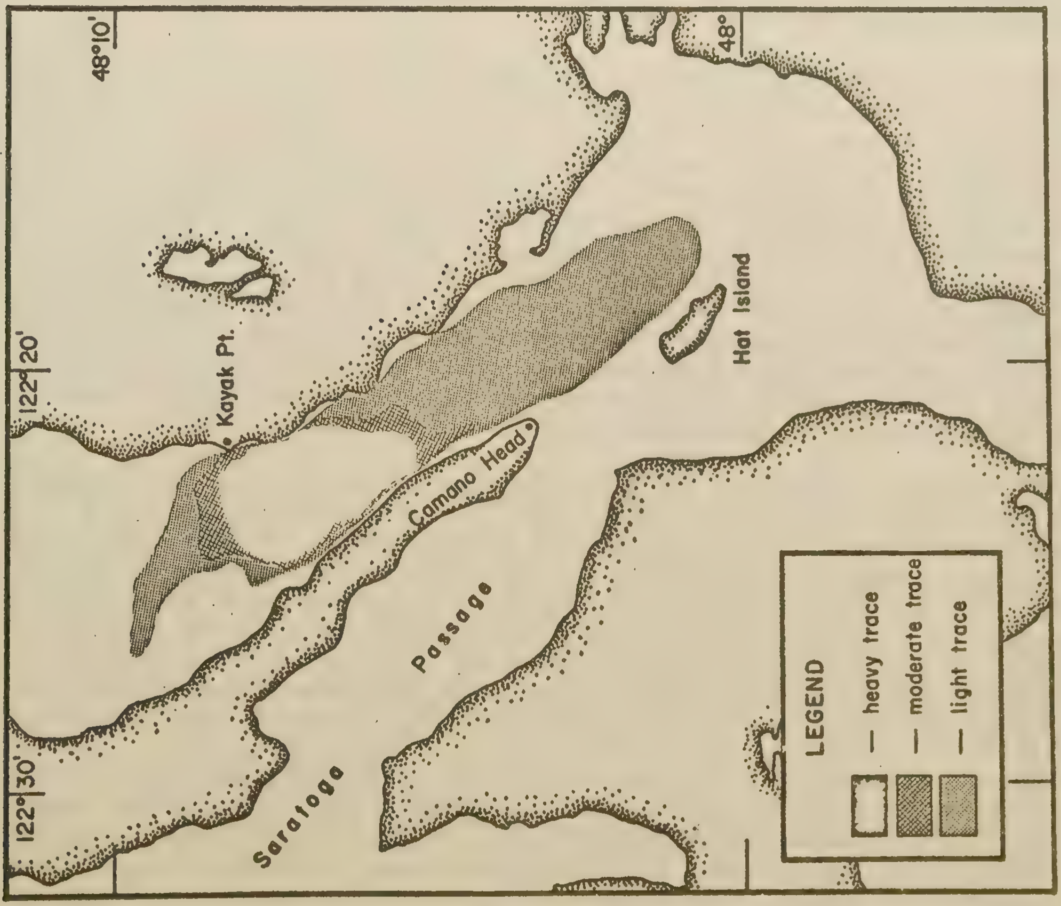
48°10'
48°
122°20'
122°30'
Kayak Pt.
Hat Island
Camano Head
Saratoga
Passage
LEGEND
— heavy trace
— moderate trace
— light trace

Fig. 6 Distribution of hake school in Port Susan, Washington on March 22-23, 1967.

of the diel vertical distribution and migrations of this species has demonstrated that it is found near the seabed during the daylight hours, migrates toward the surface during the early part of the night, concentrates near the surface between 2400 and 0300 hours and migrates into deeper water with the onset of daylight (Fig.7). The diel migration of this euphausiid is similar in timing to that noted for the Pacific hake (Fig. 8) and suggests the possibility that the diel migration and daily schooling patterns of Pacific hake may be largely influenced by the distribution and abundance of its food.

7 DESIGN OF FISHING STRATEGY

When considering the design of recommended fishing strategy as a product of information retrieved extensively from research surveys, several key factors will govern ultimate harvest decisions. These include distribution and concentration of mass in time, seasonal aspects of migration and the behavior of the exploitable stock elements. These factors must be evaluated to attempt to provide answers to the basic question of (1) where should fishing be concentrated, (2) how should fishing be conducted (by what gear types), and (3) in what time periods should fishing be undertaken so as to minimize extraction cost and maximize the theoretical potential yield. The total forecasted yield will also have an important bearing on the number of units to be deployed and the period that they will be active. In evaluating the above factors, decisions must be made regarding logistics to the raw material source, availability of the resource to extant fishing gears, and the probability of locating and detecting concentrations within the zoogeographic range. With the above discussion of factors to be considered, let us review the basis for decision and the resultant fishing strategy that evolved for Pacific hake.

For U.S. fishermen a potential raw material supply was in a relatively close operational radius of key coastal ports from San Diego, California to Seatte, Washington. During the spring, summer and fall, the adult population could be exploited effectively by boats operating out of northern ports while in the winter period there was an opportunity for the species to be exploited by fishing vessels operating out of ports in southern California. During the period that the adult population inhabited the Continental Shelf, bottom trawl gears could be deployed to harvest the species, although segments of the population were not available to this type of gear, particularly at such times that the schools congregated 10 m or more off bottom. In the southern portion of the geographic range when the adult stock were spawning, the existing gear that might have been used was midwater trawls. At such time the hake schools were farther offshore over relatively deep water and their density levels may prohibit effective exploitation with existing midwater gear.

The problem of locating and detecting schools of hake in the northern portion of the range during the spring, summer, and fall period was easier as the search area was relatively confined and the numbers of schools large. On the other hand, locating and harvesting schools of hake during the spawning period appears to be much more difficult. The areal distribution of hake at this time appears to be much greater and the schools much less vulnerable. With these factors in mind, it appeared more desirable to initiate fisheries exploitation in the more northern part of its range off Oregon and Washington during the period when the species was closer inshore, could be more easily detected, and could be harvested with existing extraction technology.

From the standpoint of strategy of removal, however, one major problem remained as regards to the initiation of a U.S. fishery; that is, how could the species be harvested in large volumes at relatively low cost. It was possible to harvest hake with existing bottom trawl gears in large quantities, but there were periods when the hake schools were completely unavailable to this type of gear. As a consequence, American investigators designed and developed a "Universal trawl" that could be fished both on and off bottom, thus allowing the fishermen to exploit the hake schools regardless of their vertical distribution pattern. The effectiveness of the gear, however,

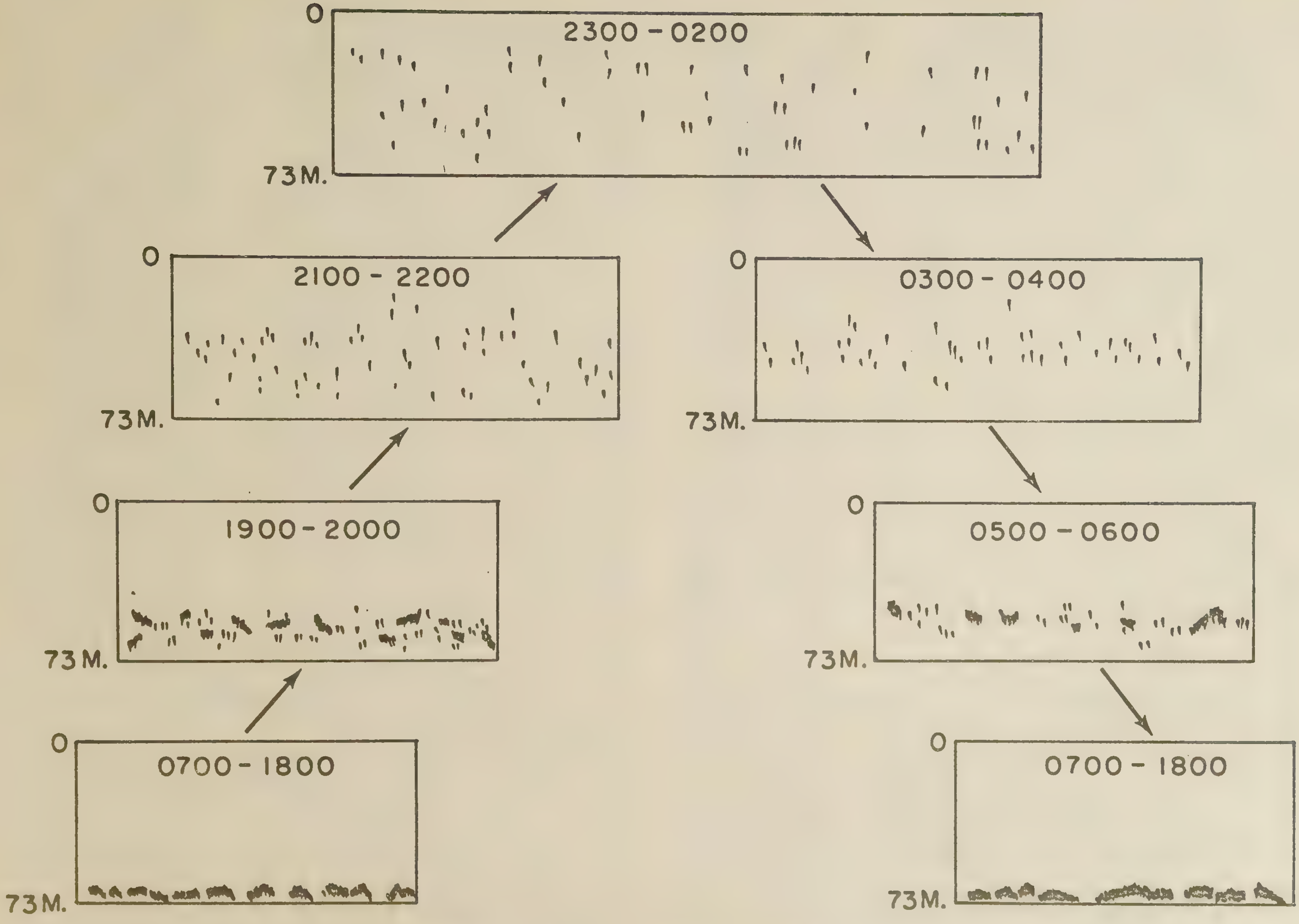
2300 - 0200
2100 - 2200
0300 - 0400
1900 - 2000
0500 - 0600
0700 - 1800
0700 - 1800
0
73M.

Fig. 8 Diagram showing diel movement of hake (Merluccius productus) off the Washington coast.

required precision depth control and hence the ultimate development of a telemetering system which allowed accurate positioning of the net in the water column.

The design of an effective Universal trawl required careful consideration of the geometric form desired with particular emphasis on achieving optimum cross-sectional area at the mouth of the net. A trawl, being a non-rigid harvesting device, lends itself to some rather interesting speculations on how the change in shape of the mouth of the trawl might affect harvest. Fig. 9 and 10 provide an indication of the changing cross-sectional area sampled by trawls having different geometric shapes but having the same perimeters or circumferences. The best shape is obviously a function of the schooling and density patterns of the fish being sought, particularly in a vertical sense. In those instances where there is rather homogeneous density pattern of schools aggregated above the seabed as the net attains a circular shape in the mouth, it will have the greatest cross-sectional area and thus the most effective harvesting tool. In those instances, however, where density increases rapidly when one approaches the seabed it might be desirable to alter the net shape to achieve a more eliptical form and hence increase the horizontal axis of sampling. The net would thus assume greater horizontal spread while decreasing the vertical height of the net. Of course the effectiveness of this maneuver depends on the rate which density changes with depth as compared to the changes in the functional fishing area of the trawl.

Thus, American investigators found it appropriate from an initial standpoint to exploit the species in the more northern portion of the species' range and to design a gear-type consistent with the behavior patterns of the species. Because of the seasonal migration patterns of the species, the season of operation was confined to the period May through November when the fish concentrated over the Continental Shelf and detection probability was high. In a diel sense, fishing was recommended to be conducted during hours of daylight. The dispersion of fish at night has so far precluded effective exploitation during this time period.

From the standpoint of the evolution of Soviet fisheries, the raw material source was at great distance from home ports and any consideration of exploitation would require a large support fleet to maintain fishing operations. It is obvious that the mature stock during the May through November period was closer to home ports and if it could be effectively exploited during this period it would reduce operational costs. Because of the larger size of Soviet fishing vessels and their trawls, the hake stocks were generally available (during the May to November period) to the high-rising bottom trawls used by the Soviet fleet. Effective winter exploitation, however, would require exclusive use of midwater trawls such as used by the U.S. fleet. The development of the Soviet industry, as with the U.S., has initially been based on the exploitation of the mature stock in the northern portion of its geographic range. They have, however, taken a different route as regards to exploitation of off-bottom schools. Part of their fleet has been equipped with large two-boat midwater trawls and part of the fleet has employed standard bottom trawl fishing techniques. The strategy here being to have both types of gear available so that regardless of the vertical distribution patterns of schools they can be exploited by some segment of the fleet. Soviet vessels, as well as those of the U.S., have generally confined their operations to daylight hours, although some night fishing has apparently taken place.

Because of the highly changing characteristic of hake schools and their diel movements, fleet operations have allowed for maximum retrieval of information concerning distribution patterns and if this information is analyzed, it can be used to re-assess effective deployment of the fishing units. This has a definite advantage in the Soviet fleet where a large number of vessels (50 to 100) are being utilized to exploit the resources. It in a sense enhances the location and detection probability.

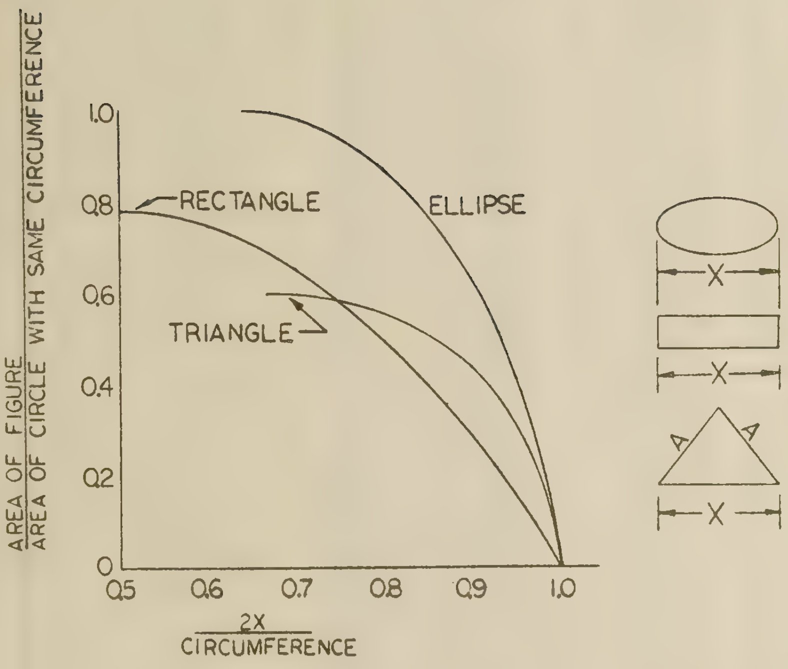

Fig. 9 Relation of various geometric forms with constant perimeter and changing height.

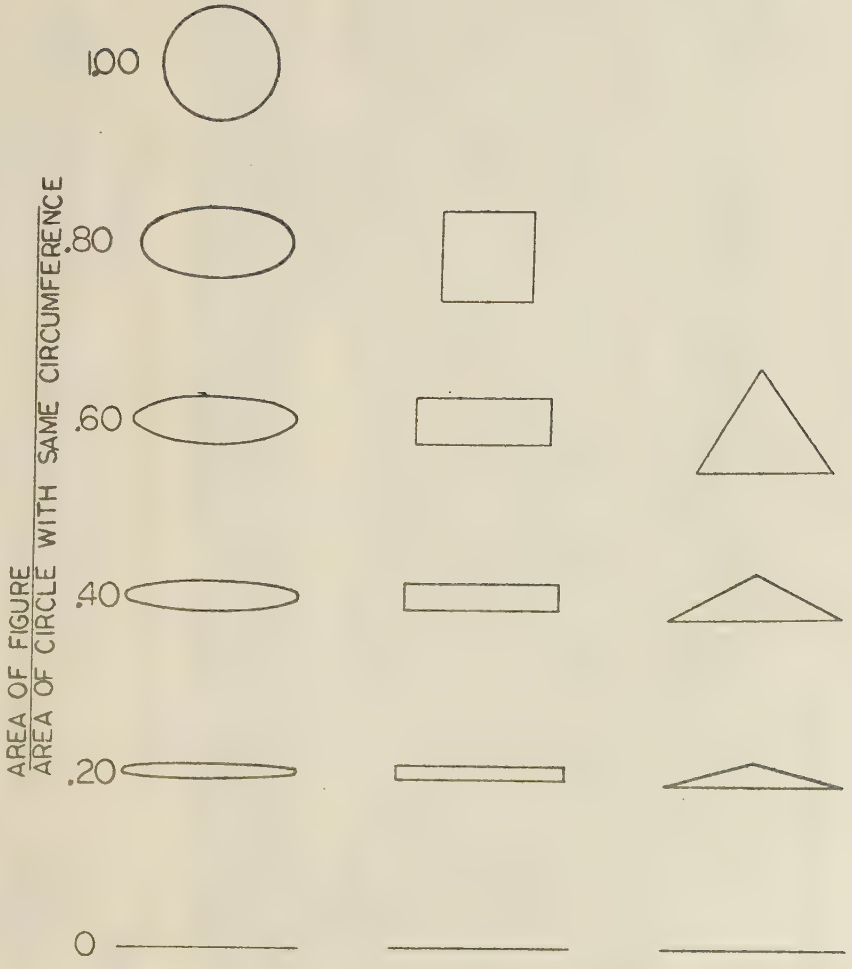
AREA OF FIGURE / AREA OF CIRCLE WITH SAME CIRCUMFERENCE
1.00
.80
.60
.40
.20
0

Fig. 10 Decrease in area sampled of three geometric forms under conditions of constant perimeter with change in "X".

8 DESIGN OF FISHING RATIONALE

I have previously noted that the exploitable stock size off Oregon and Washington was forecasted to range between 130 and 260 thousand metric tons. This preliminary estimate then can be used as a basis to establish fishing pressure which should be exerted during the early phase of fisheries development. This information along with the general distribution pattern of the stock components; that is, that the younger age classes are not generally inter-mixed with the mature exploitable stocks in the northern portion of the range, allows one to make another recommendation for geographic distribution of fishing. That is, fishing conducted in the more northern segment of the species geographic range should minimize loss or damage to the smaller rapid-growing portion of the population. It would appear from evaluating the growth pattern of the species that the critical size would occur at approximately age three. That is, growth in weight of a year class would exceed losses due to mortality up to at least this age. As most of the fish taken in the commercial fishery off Washington and Oregon are four years of age or over, there appears to be little problem of diminishing the potential to extract the maximum sustainable yield based on growth and mortality functions.

Development of more effective detection systems and midwater trawl gear may ultimately lead to exploitation of the offshore spawning stock. Here too there are no immatures, and assuming that a stock recruitment problem does not occur, then fishing pressure could be adjusted to theoretical yield based on the growth and mortality functions alone.

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The author is indebted to Bert Larkin of the Seattle Biological Laboratory for the information used concerning the age frequency and growth pattern of Pacific hake.

E/12

ECHO SOUNDING OBSERVATIONS OF FISH BEHAVIOUR IN THE PROXIMITY OF THE TRAWL

by

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Abstract

Echograms of fish school behaviour (herring, sprat, horse mackerel and sardinella) in the proximity of two-boat pelagic trawl were recorded.

OBSERVATIONS AU SONDEUR A ULTRASONS SUR LE COMPORTEMENT DU POISSON A PROXIMITE DU CHALUT

Résumé

La communication présente des échogrammes du comportement de bancs de poissons (harengs, sprats, chinchards et sardinelles) au voisinage d'un chalut pélagique tiré par deux bateaux.

OBSERVACIONES DE SONDEO POR ECO SOBRE EL COMPORTAMIENTO DE LOS PECES EN LAS PROXIMIDADES DE LA RED PARA PESCAR AL ARRASTRE

Extracto

Se registraron ecogramas del comportamiento de los cardúmenes (arenque, sardineta, jurel y sardinella), en las proximidades de una red de arrastre pelágica remolcada por una pareja.

1 INTRODUCTION

The development of fishing gear and particularly of active pelagic gear depends on a knowledge of fish behaviour and the behaviour of fish schools.

For 20 years various underwater detection devices, photographic, television apparatus and underwater craft have been used which permit the observation directly or indirectly of the behaviour of various types of fish. Besides this equipment, observations are made on the behaviour of fish in experimental conditions specially created for that purpose, mainly to follow reactions difficult to observe with the above apparatus in natural conditions.

2 REACTIONS OF FISH SCHOOLS CLOSE TO THE TRAWLNET

The use of an echo sounder for investigations of the behaviour of fish in the proximity of a net is an important part of a program which may help improve the construction of fishing gear or at least to explain its action in particular fishing conditions.

Here are the results of observations on fish behaviour in close proximity to the two-boat pelagic trawl as well as some interesting observations on fish concentration caused by various environmental conditions. Experiments were carried out in the Skagerrak on the behaviour of herring schools and their reaction to the two-boat trawlnet. Observations were made from a third boat which checked the position of the two-boat pelagic trawlnet relative to the fish schools. The observations were carried out at night when the fish schools were in the surface layers and were more scattered than by day.

There were no significant catches with a vertical mouth opening of 10 to 12 m and a towing speed not exceeding 3 knots. It was only when the two-boat trawlnet had a vertical opening of 16 to 20 m that catches were made.

The echograms shown here illustrate the relationship of the net to the fish schools. They have been chosen from among many that were obtained by a third vessel which approached the two-boat trawlnet from the codend direction. The speed of the third vessel was slightly greater than that of the towing vessels. When the observer vessel was over the net mouth its engines were stopped, permitting the towed gear to pass slowly underneath. In this way it was sometimes possible to register the opening of the net on the echogram for quite a while.

The echograms show three various positions of the net compared with the fish school. The first echogram (Fig.1) shows the mouth of the two-boat trawl in the center of a layer of fish, or, it could be said that the net attacked the fish school at its center. Then the herring scattered upward and downward, leaving an empty area in the middle where the net had been towed through a few minutes earlier. In the mouth of the two-boat trawlnet, over which the observing vessel had been for more than a minute, there were traces of fish, principally under its upper part.

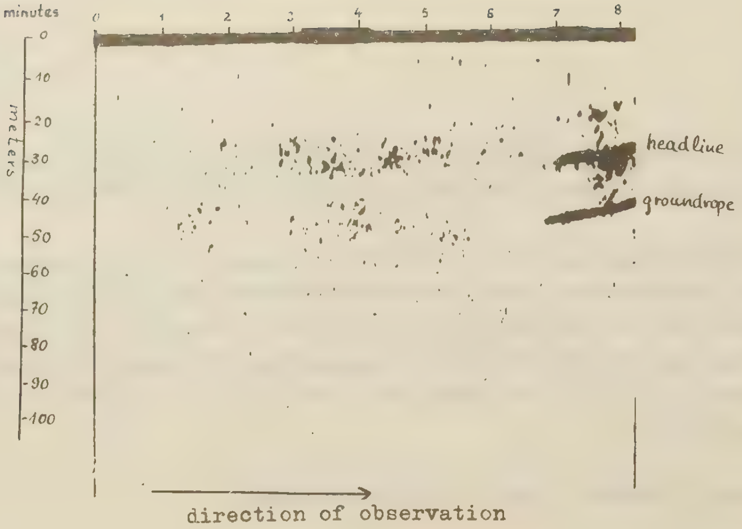
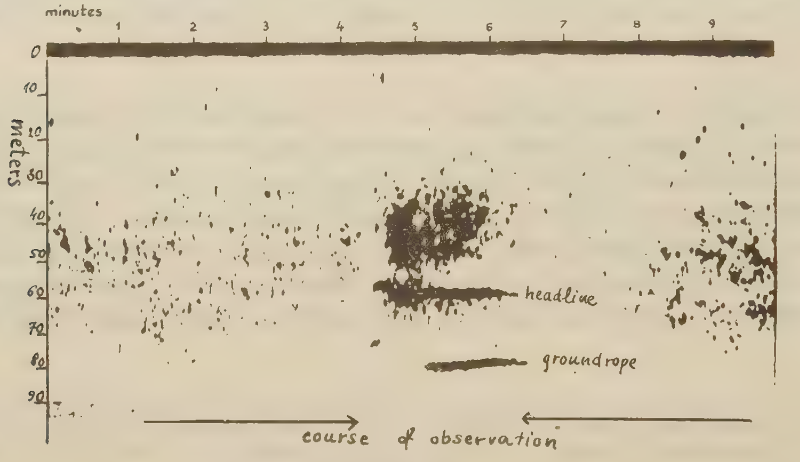


Fig. 1 Location: 30 mi NW of Skagen, Skagerrak Species: herring
Date: February 1955 (night) Gear: 2-boat trawl



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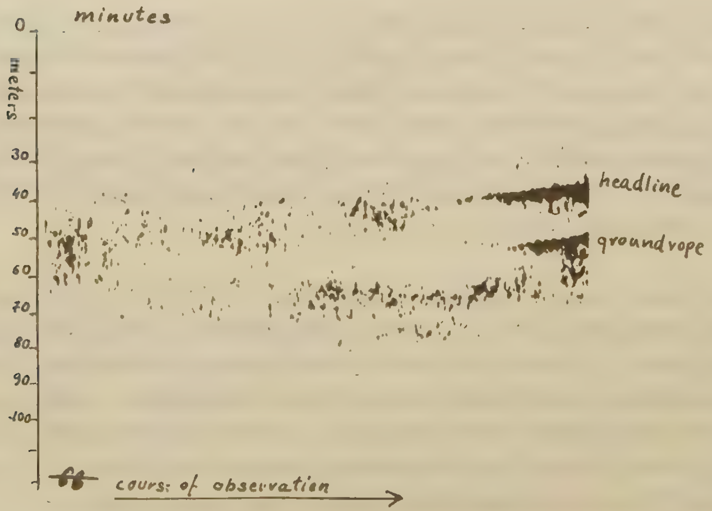

Fig. 3 as for Fig. 1

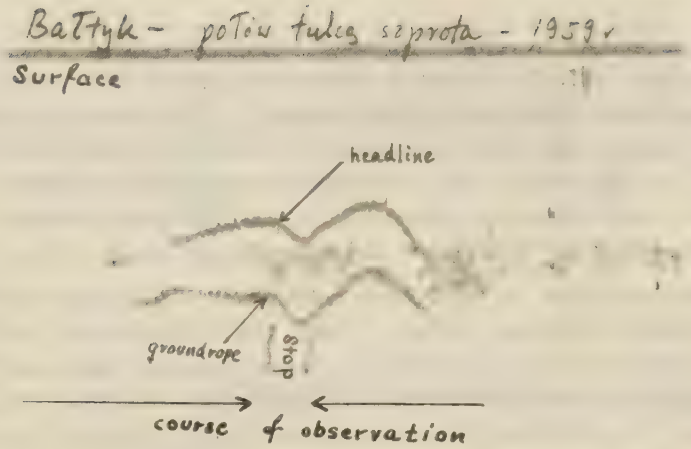

Fig. 4 Location: Gulf of Gdansk Species: sprat
Date: March 1959 (day) Gear: 2-boat trawl

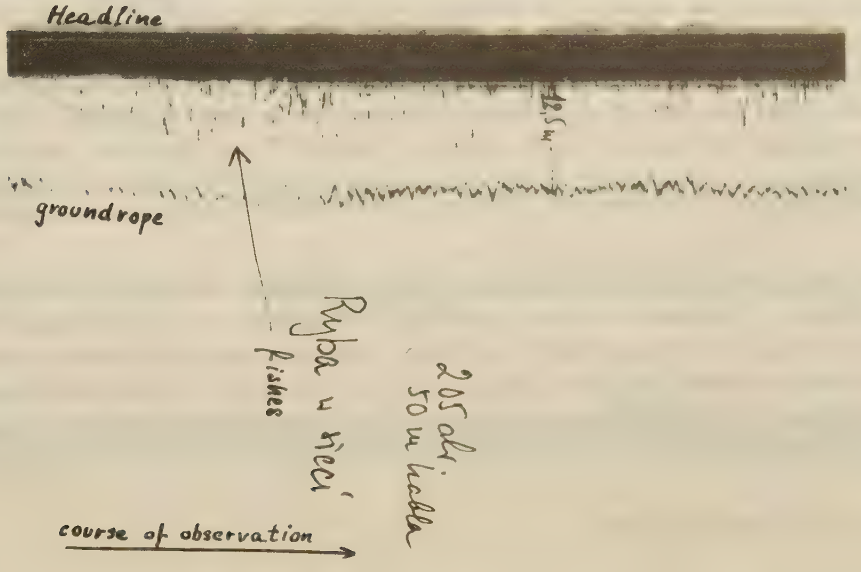

Fig. 5 Location: St. Luiz Canyon, Senegal Species: Sardinella, horse mackerel
Date February 1966 (night) Gear: 1-boat trawl

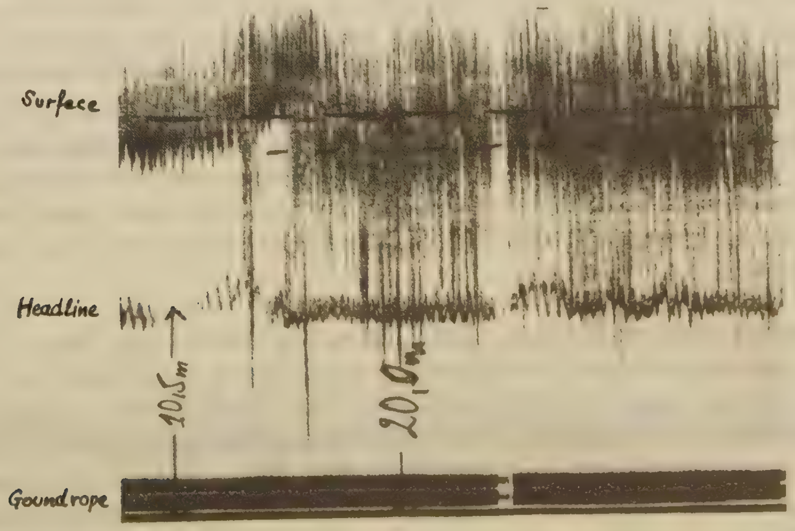

Fig. 6 as for Fig. 5

The second echogram (Fig.2) shows a situation where the mouth of the two-boat trawlnet attacked the lower part of a fish school. This caused the fish to escape mainly upward. Here again the fish are found within the limits of the net mouth and under the upper part of the net. The concentration in the middle over the net mouth appears bigger than it actually was because it was recorded twice as the observing vessel moved up over the two-boat trawlnet and then back again. Fig. 3 echogram seems to give the most precise position of the fish school in relation to the two-boat pelagic trawlnet which attacked its upper layer. From the codend side we may observe on the echogram that the school at the beginning is more compact and corresponds to the average density of concentrations found there, then nearer to the net mouth the school becomes more scattered. Just behind the net is an empty area without fish, showing that the net had passed there. Behind the mouth there are some weak contours of the other parts of the net, showing that the net was in a nearly horizontal position. The fish school in this case also showed an escape response and mainly gathered under the lower part of the net. Inside the opening of the net we note the presence of fish, here again under the upper part of the two-boat trawlnet. In this echogram we can most distinctly note the return of scattered herring to a more compact concentration. This feature is estimated to happen in a lapse of about five minutes, which means that when the net is moving at a speed of three knots this takes place at a distance of about 450 m behind the net.

The next echogram (Fig.4) concerns sprat catching in the Baltic Sea, also with a two-boat trawlnet. Contrary to the previous echogram we do not deal here with a quick reaction of the fish, although the two-boat trawlnet was not opened more than 15 to 16 m and the towing speed varied little from 2.5 knots. This slow speed caused the sagging of the net in its aftermost parts. This echogram was also taken by a third vessel.

3 TRAWLING NEAR THE SURFACE

The next experiments were carried out with the use of a net echo sounder during experimental catches with a pelagic trawlnet in West African waters. The echograms (Figs. 5 and 6) show the net's attack on the schools near the surface at night. In Fig.5 the net echo sounder is mounted with the oscillator fixed to the headline and in Fig.6 the oscillator is fixed to the footrope. The explanations given along with these figures show the position of the pelagic trawlnet. The vertical opening in the first case was 12.5 m and 10.5 m in the second. Near the mouth the presence of quite scattered fish can be seen in the first echogram but no fish are seen in the second. Fig. 6 also illustrates another feature, the disturbance caused by the propeller 140 m from the stern of the vessel.

The disturbance reached a good depth, greatly exceeding 10 m. In the same echogram there is a section without disturbance registered but there is no trace of fish either. We may deduce that catches very near the surface are possible if they are not carried out in the propeller wake. The results of the experimental catch (Fig.5) were 3 tons of fish (horse mackerel, sardinella), the fish being registered during a period not exceeding one hour. In this echogram too we see a concentration of fish in the upper part of the trawl mouth. Although here the vertical opening was much smaller than in the Skagerrak, the towing speed was much greater, exceeding 4 knots.

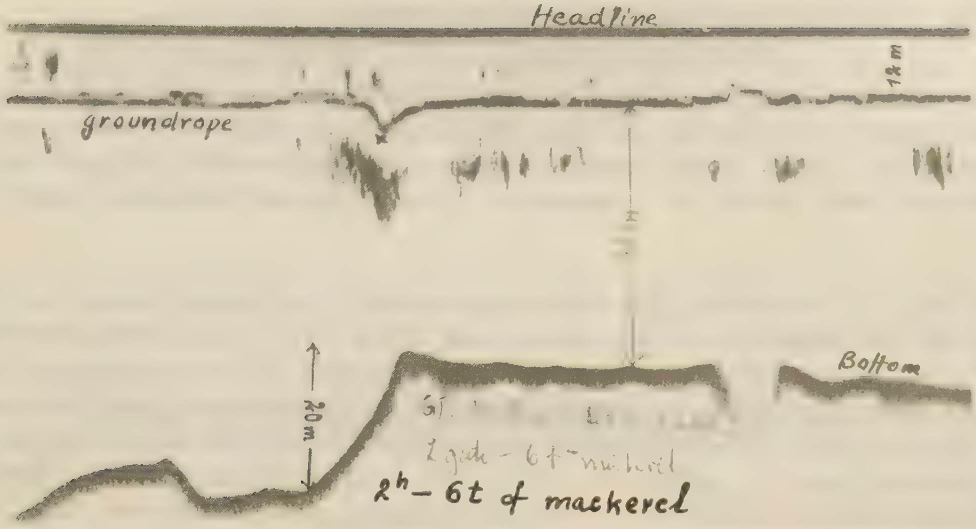

Fig. 7 Location: Dakar, Senegal Species: mackerel
Date: November-December 1966 (dusk) Gear: 1-boat trawl

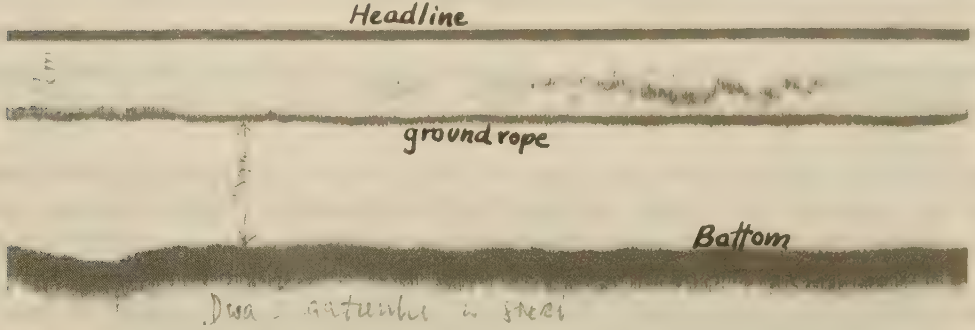

Fig. 8 Location: Dakar, Senegal Species: mackerel
Date: November-December 1966 (day) Gear: 1-boat trawl

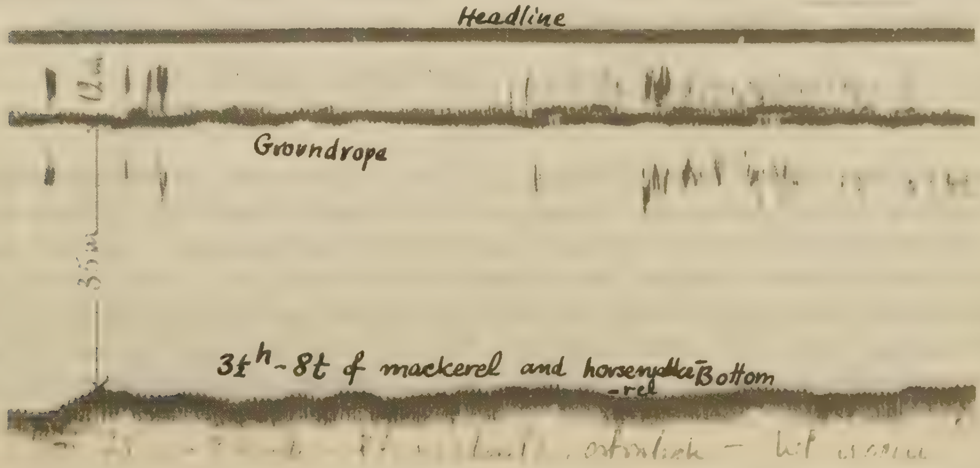

Fig. 9 Location: Dakar, Senegal Species: mackerel
Date: November-December 1966 (dusk) Gear: 1-boat trawl

4 TRAWLING ON CONCENTRATIONS OF MORE THAN ONE SPECIES

The next series of echograms (Figs.7,8 and 9) show two problems : the simultaneous presence of two species of fish in the same demersal zone, and the reaction of fish to the pelagic trawlnet. These three echograms were made in December 1966 on the same fishing grounds off West Africa by a commercial fishing vessel equipped with a net echo sounder.

Echogram (Fig.7) illustrates the situation where, after having seen that there were less fish in the proximity of the mouth than below it, the net was lowered much deeper (20 m) so that the concentrations might be attacked by the trawlnet. As seen in the echogram (from the mark 'x') the bottom echo has approached the footrope by 20 m, but in spite of that the distance of the fish concentration from the net has not lessened, but stayed about 5 m under it. The fish were probably mackerel for two hours fishing resulted in a catch of 6 tons of mackerel. The catch was then of commercial value, though more fish appeared to escape below the net than went into it. A similar situation is presented in echogram (Fig.9) where the distance of the fish from the net resembles those in the echogram (Fig.7). Again the schools are located half in the net and half below it. Also in this echogram we have to deal with another species which remains almost entirely within the limits of the mouth of the pelagic trawlnet. The catch results of 8 tons in 3.5 hours showed that horse mackerel were present besides mackerel. It should be stressed here that the two species probably reacted differently to the action of the net, as indicated by what follows:

Echogram (Fig.8) shows that two species may live in one pelagic zone simultaneously. Here the species are horse mackerel and sardinella. Both species are enclosed by the mouth of the net and neither shows such mobility as the mackerel in Figs.7 and 9.

The series of three echograms (Figs.10,11 and 12) are not observations of fish behavior directly related to fishing gear but they do further illustrate the preceding statement that mixed fish concentrations occur in the demersal and in the pelagic zones. The echograms are from the Baltic Sea. Fig.10 shows concentrations of herring and sprat. Fig.11 represents a concentration of spawning cod and herring. Fig.12 shows a concentration of two or three ages of herring. These conclusions have been drawn from commercial catches in areas where the echograms were recorded.

5 DEMERSAL FISHING WITH PELAGIC TRAWL

The last series of echograms (Figs.13,14 and 15) concern experiments carried out in African waters during demersal fishing with a pelagic trawlnet. These experiments were aimed at testing the wider application of this fishing gear. In all cases the oscillator of the net echo sounder was placed on the headline. The bottom echo and the echo of the footrope merge when the footrope rests on the bottom (Fig.15). The other two echograms were made when lowering the net towards the bottom by paying away the trawl warps, thus the apparent raising of the bottom echo. The vertical opening of the pelagic trawl was 11 to 12 m and the towing speed was about four knots.

The echogram (Fig.13) which illustrates the behavior of serranids shows that the bottom, before being touched by the footrope of the pelagic trawlnet does not show any

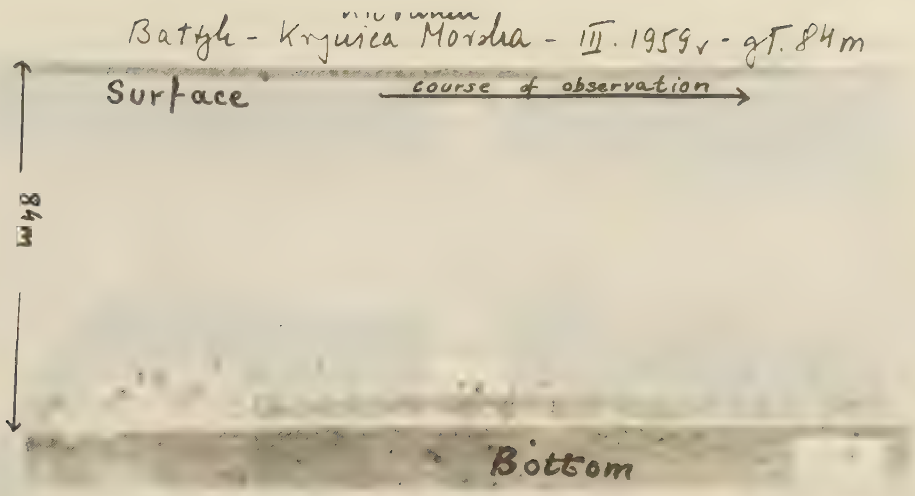

Fig. 10 Location: Gulf of Gdansk Species: herring, sprat
Date: May 1959 (day)

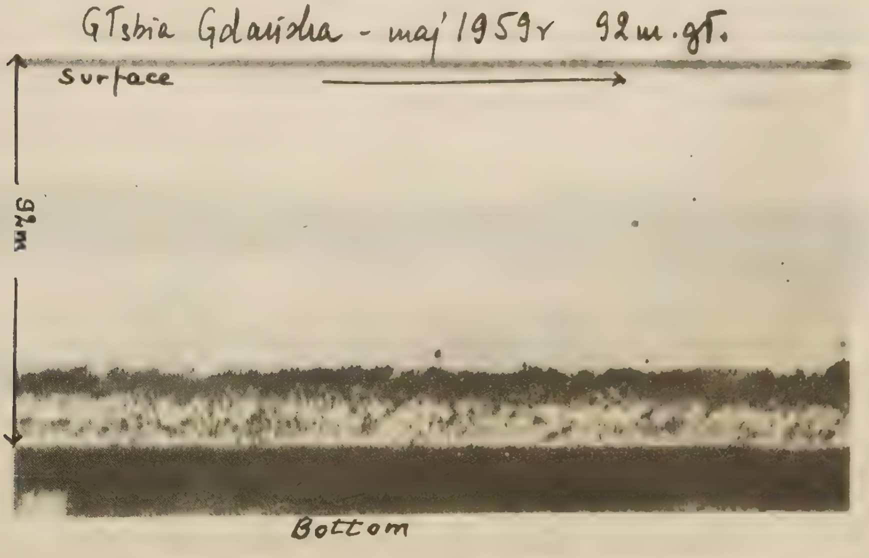

Fig. 11 Location: Gdansk Deep Species: cod and herring (spawning)
Date: May 1959 (day)

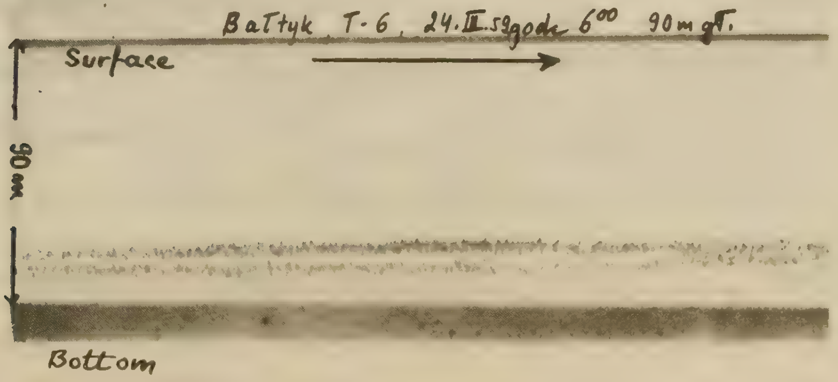

Fig. 12 Location: Gulf of Gdansk
Date: March 1959 (day)

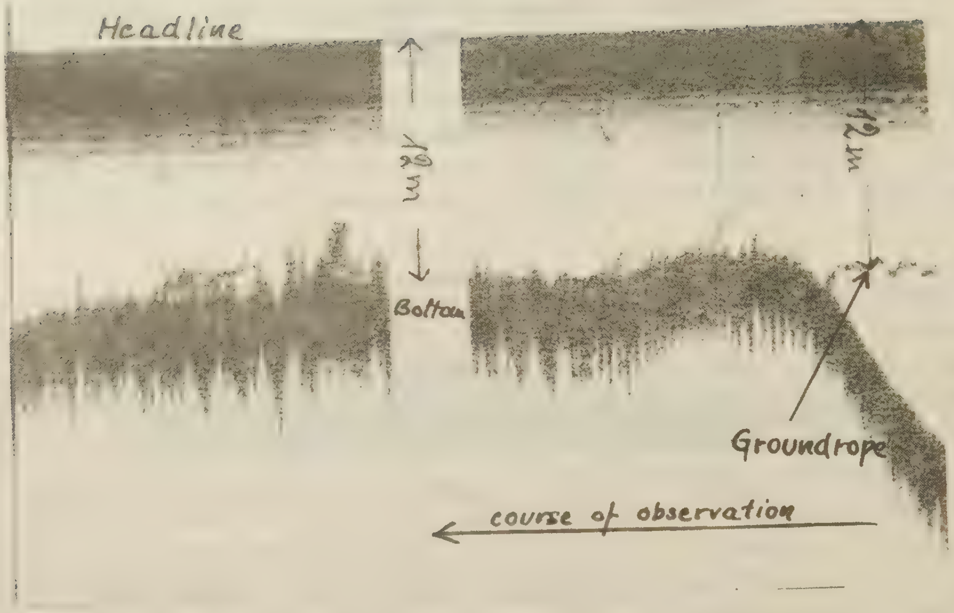

Fig. 13 Location: St. Luiz Canyon, Senegal Gear: 1-boat trawl
Date: February 1966

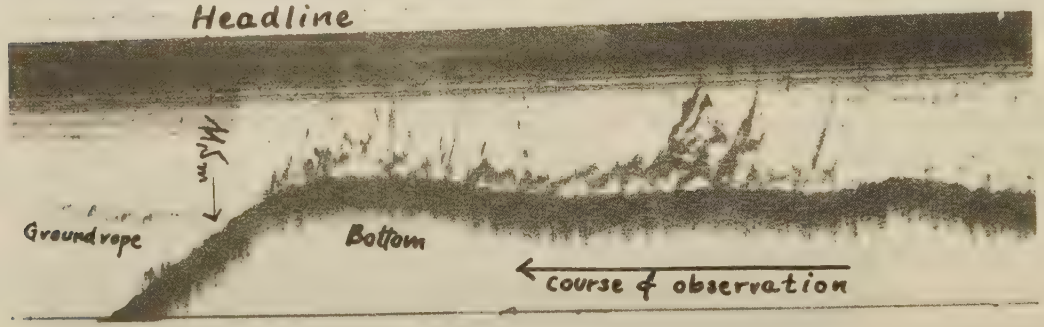

Fig. 14 as for Fig. 13

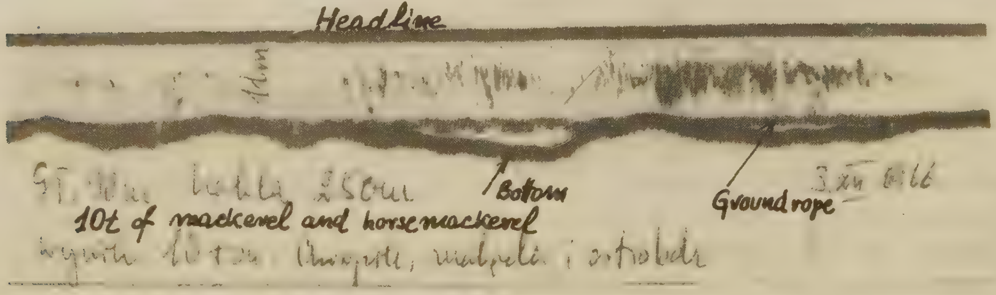

Fig. 15 Location: Dakar, Senegal Species: mackerel, horse mackerel
Date: December 1966 (day) Gear: 1-boat trawl

apparent fish present, nor was there any trace of fish on the ship's echo sounder (Kelvin Hughes MS 29) which had recorders. However, when the footrope touched the bottom, the demersal zone becomes singularly animated. The escape of fish disturbed from the bottom reaches several meters upward. This feature is even more distinct in the next echogram (Fig.14) where some fish, in their attempts to escape, almost reached the top of the upper part of the net. In principle, it is possible to observe the escape of particular individuals or of a group of fish in the upper layer of the schools. Some of them remained for a time within the range of the oscillator and then either slipped back towards the codend or passed out beyond the mouth of the net. As shown by the catch results, they were cutlass fish and a large part of them were in the codend and another part were entangled in the upper netting of the trawlnet. During the experiments it was found possible to keep the desired distance of the footrope of the pelagic trawl from the bottom and to carry out directed fishing by checking both the echograms of the echo sounder on the fishing vessel and on the net echo sounder.

These operations may be carried out at various depths by changing the length of trawling lines and towing speeds. This in turn requires continuous monitoring of the underwater detecting devices and immediate action by the crew at a given order.

6 CONCLUSIONS

The material contained in the echograms permits certain conclusions to be drawn regarding the behavior of fish and their exploitation:

(i) Fish schools respond by escaping from the center of the disturbance - in this case from the net. As to the direction of escape, it is the position of the attacking gear in relation to the fish school that is the main deciding factor. The attacked school disperses from the center upward and downward and supposedly sidewards but this has not yet been confirmed by the echo sounder. When the school is attacked at its lower edge the fish mainly escape upwards, whereas attacked from the upper edge, the fish mainly escape downwards

(ii) The fishing efficiency of the two-boat trawlnet or of the pelagic net depends mainly on the size of the mouth opening which must be greater, the slower the towing speed

(iii) Less active species with weaker swimming abilities, e.g., sprat, do not require such large mouth openings as do quick fish and the towing speed may therefore be much less

(iv) Fishing in surface layers with a pelagic trawlnet is possible but the track of the screw must be avoided and this can be done by frequent changes in course

(v) The pelagic trawlnet or the two-boat trawlnet may be used in demersal fishing on the bottom

(vi) Concentrations of several species which appear simultaneously may be found in the same aphotic layer and in the demersal layer and may be caught by pelagic trawlnets

(vii) The net echo sounder, as a standard part of the equipment of a commercial fishing vessel, may be used for further observations of fish schools to improve catch efficiency, as well as to carry out scientific research

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THE INFLUENCE OF FISH BEHAVIOUR ON THE CHOICE OF THE TRAWL NET SHAPE AND SIZE

by

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Abstract

Commercial fishes can be divided into three ecological groups according to the zones where they usually dwell: on the bottom, near the bottom and in the upper and intermediate layers of the sea. Some aspects of designing trawlnets for better exploitation of these fishes are considered.

E/13

INFLUENCE DU COMPORTEMENT DU POISSON SUR LE CHOIX DE LA FORME ET DES DIMENSIONS DU CHALUT

Résumé

Les poissons recherchés par la pêche commerciale peuvent êntre rangés en trois catégories écologiques, selon qu'on les trouve généralement sur le fond, à proximité de celui-ci, ou dans les couches supérieures et intermédiaires de l'océan. La communication examine certains aspects de la mise au point de chaluts conçus pour améliorer la capture de ces poissons.

LA INFLUENCIA DEL COMPORTAMIENTO DE LOS PECES SOBRE LA ELECCION DE LA FORMA Y EL TAMAÑO DE LA RED DE PESCA AL ARRASTRE

Extracto

Los peces comerciales se pueden dividir en tres grupos ecológicos, según las zonas en que generalmente habitan: se el fondo, cerca del fondo y en las capas superiores e intermedias del mar. Se consideran algunos aspectos del diseño de redes de pesca al arrastre para una mejor explotación de estos peces.

1 INTRODUCTION

The question of a suitable size and shape for trawlnets is not new. Remarkable progress has been made in improving dragging gear and in its differentiation according to the type and character of its work since 20 years ago. The development of underwater detection instruments and the direct observation of the fish behaviour in the proximity of the fishing gear have helped this progress.

Understanding these direct and indirect observations has led to much development in the construction of fishing gear. The greatest attention has been given to pelagic trawling gear. This was rendered possible by development of research on the basic service parameters of trawling gear. To that end a large number of instruments have been used, which, in a significant way, have helped to deduce the shapes taken by the gear in operation.

This question is, however, fairly complicated as different species caught commercially may be characterized by a variable distribution in the pelagic and bottom zones and by different responses to the action of fishing gear. This problem cannot usually be considered separately for each species of fish, as it would multiply the kinds of fishing gear too much. The behaviour of fish should be considered rather according to ecologic groups with the aim of finding affinities in their reaction. Insofar as certain species of fish are concerned there is total lack of observations but it is still reasonable to assume a priori some generalizations through such biological analogies as can help.

It is proposed here to divide into ecological groups the types of fish commercially caught (mature individuals), according to the zones where they spend most of their existence. It also seems useful to differentiate the main factors which have an influence on the change of environment.

The analysis of the behaviour characteristics of species groups should be linked to the requirements to be met by the fishing gear. This in turn permits the choice of a given construction of the fishing gear and the tactics of handling it.

The purpose set here may seem too difficult to reach in some cases and will often have to wait for elucidation. The author, however, undertakes this problem with a view to fixing the principles which determine the lines of evolution of fishing gear and to start a discussion by analysing the controversial viewpoints in this field. It is proposed to adopt the following division of fish into ecologic groups and to define the limits of zones for their exploitation.

2 DIVISION OF FISH FAUNA INTO ECOLOGIC GROUPS

(A) Demersal fish lying on the bottom or burrowing into it

(B) Demersal fish living near the bottom

(C) Pelagic fish living in the intermediate layers of the water

These are the pendant zones of exploitation for these ecologic groups:

(a) The demersal zone up to 0.5 m above the bottom

(b) The demersal zone up to 10 m above the bottom

(c) The pelagic zone

The above division is not accurate though it is based on habits of fish living in the stated zones which show the body shape adapted to their way of living in a given environment. The shape of flat fish and skate shows that they seldom leave the bottom environment, they do not cover longer distances quickly and they have a relatively sedentary life. On the other hand, cod or grouper are better swimmers; they can make longer migrations and the shape of their body confirms this. Representatives of pelagic fish have a streamlined shape and strong muscles which permit them to quickly make great diurnal as well as seasonal migrations.

The appearance of representatives of groups "(B)" and "(C)" in the two zones in some definite conditions is a frequent feature. Group "(A)" includes, in particular, flatfish, skates, sand-launce and angler.

Group "(B)" comprises mostly such families as: Gadidae, Scorpenidae, Sparidae, Scieanidae, Serranidae, and so on. Group "(C)" comprises Clupeidae, Engraulidae, Scombridae, Carangidae, and Thunnidae.

3 INFLUENCES ON THE CHANGE OF LIVING ZONE

The factors which influence the choice of living zone are biotic, mainly spawning and feeding, and physico-chemical like temperature, light, salinity and oxygen content.

Let us try to estimate the action on the particular ecologic groups of fish of these factors which cause a change of living zone. The following table is proposed to that effect with the following signs:

- causes no change of zone

+ causes a change of zone

-+ may cause a change of zone

Group	Biologic factors		Physico-chemical factors			
	spawning	feeding	light	temperature	salinity	oxygen
"A"	-	-	-	-	-	-
"B"	-	-+	+	-+	-+	+
"C"	-+	-+	+	-+	-+	+

If in group "A" for example, the fish do not respond to the changes in oxygen content and salinity, it means that the above changes in given conditions do not force the fish to leave the bottom zone but may cause some shifting of their living area in a horizontal direction.

In a similar way it is possible to try to estimate the degree of response of the particular groups to the various disturbances in the environment according to the following scale:

+++ strong response

++ moderate response

+ weak response

Here are given, as far as possible, distances at which it has been stated that fish were influenced:

Groups	Vibrations of the screw	Vibration of the rigging	Escape from the noticed centre of disturbances	
			In the euphotic zone	In the disphotic zone
"A"	+ several m	+	+ to 0.5 m	+ directly on it
"B"	+ 10 to 15 m	+	++ to 2.5 m	+ to 0.5 m
"C"	+++ to 30 m	++	+++ to 5.0 m	+ to 1.0 m

Sometimes there are essential differences in the degree of response of the particular types of fish, even of the same ecologic group, but it seems right to register the maximum indices of this response.

This response varies greatly and depends, not only on the ecologic group of the fish or the size of particular individuals, but depends also on the location of the object which disturbs the environment and the location of the fish which is influenced. As to its significance, the reflex reaction which occurs when the disturbance has been noticed or felt is most important. A classical example is the consideration of the direction in which fish escape in the pelagic zone where the influence of the bottom need not be taken into account.

The direction of the escape depends in a great measure on the dynamic properties of the shape of the body. The general tendencies defining the habits of various types of fish of particular ecologic groups could be generalized in the following manner:

Groups	Direction of escape caused by reflex	Most frequently observed response
"A"	According to shape of body, usually downwards	Escape from disturbance centre, springing from bottom and then burrowing in it
"B"	According to shape of body, usually downwards	Escape from disturbance centre, radially in a horizontal plane and also downwards
"C"	According to shape of body, downwards and upwards, depending on the species of fish	Escape from disturbance centre, radially in a vertical or horizontal plane

It seems correct to relate the direction of the escape caused by a reflex to the shape of the body. The dynamic properties of the body, allied to the force of the muscles, give a natural, uncontrolled direction of escape. The most frequently found shape of the fish belonging to various ecologic groups and the indicated direction of the escape caused by the reflex are shown in Fig. 1.

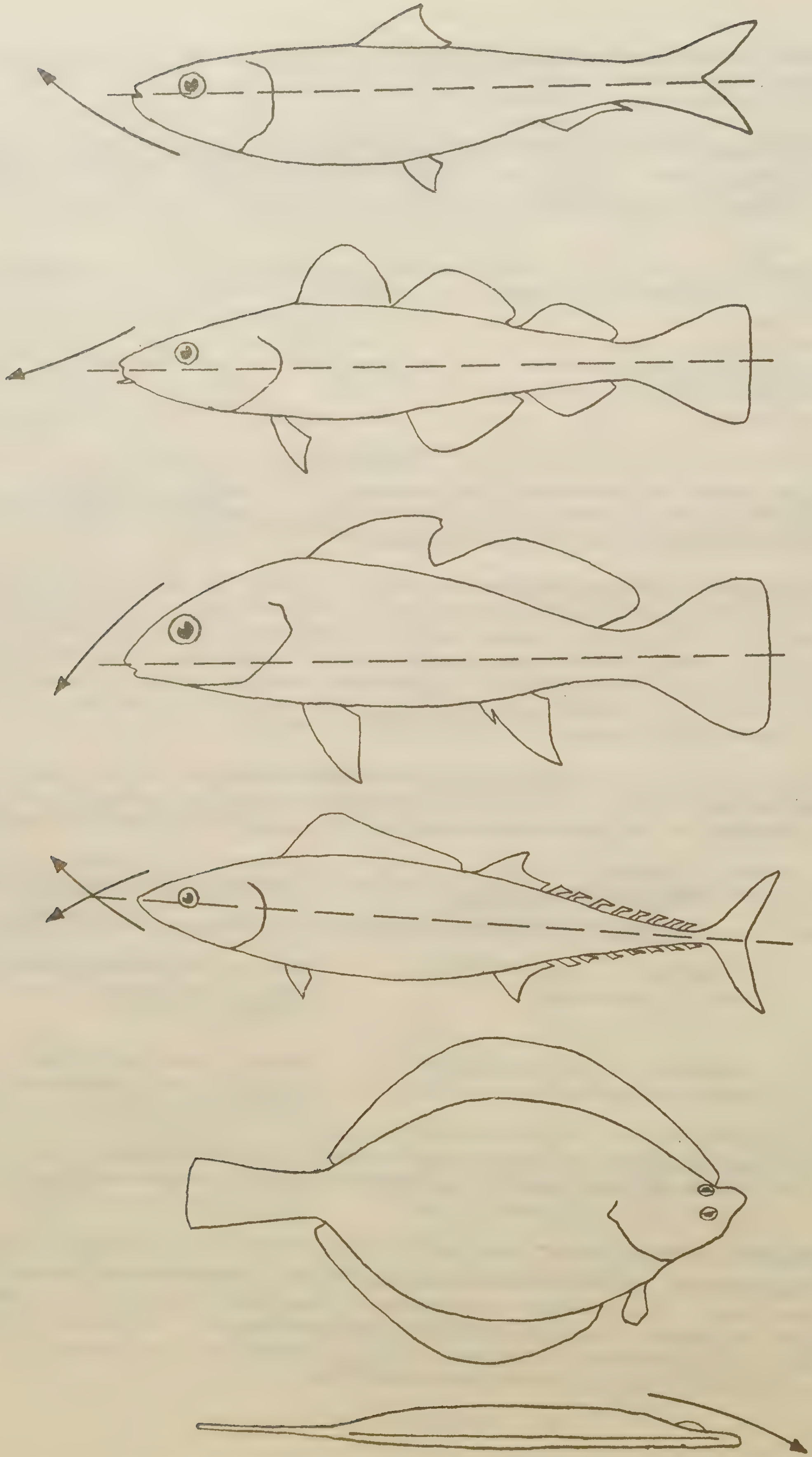

Fig. 1 The shape of fishes belonging to various ecological groups

Fish are often frightened by the source of disturbances which comes from a direction which does not permit them to utilize the dynamic properties of the shape of the body. For instance when cod or other demersal fish are attacked by the approaching trawlnet, and if the footrope adheres to the bottom they must dart upward and try to escape by swimming parallel to the bottom in a direction so as to get beyond the line of the wings. Similarly herring, as soon as they notice the approaching kite, will try to escape downward in spite of the dynamic properties of the shape of their bodies which favour an upward escape. Flatfish which keep close to the bottom may also be compelled to leave the bottom for a short while to escape the action of the fishing gear.

The swimming abilities of the particular ecologic groups and their ability to continue attempting to escape is a very significant factor when discussing the efficiency of the fishing gear and its exploitation. The data compiled from published literature permit an approximate determination of the speed of various types of fish and the distance swum without rest. The following data are tabulated for the three groups of fish along with the variations of the values concerning various types of the same ecologic group.

Group	Maximum speed per second	Distance which might have been swum without rest
"A"	5 times the length of the body	40 - 60 times the length of the body
"B"	6 times the length of the body	150 - 250 times the length of the body
"C"	6 to 8 times the length of the body	300 - 1100 times the length of the body

Relating the swimming ability to a multiple of the full length of the body seems justified, as it enables an approximate value to be determined for the particular types and sizes of individuals commercially fished.

These data are mainly based on observations made on individual fish and insofar as the school is concerned, these should be only taken as indicatives for the reaction of the school is usually slower than the reaction of the fish observed individually.

A general characteristic concerning all fish types is the reduced reaction in conditions of limited visibility or in conditions of total darkness which exist at great depths or at lesser depths when the water is turbid. Then other requirements should be met by the fishing gear.

The data having been so arranged and gathered according to its utility for trawl gear, the next step is the question of requirements which determine the shape, size and general proportions of its construction.

A summary is given below of the particular characteristics of the ecologic groups of fish which should be taken into consideration when choosing the construction properties of trawlnets.

(i) Group "A"

The fish usually do not leave the bottom, either under the influence of biological or physico-chemical factors.

The reaction caused by the action of the ship's screw is weak and occurs at a distance of a few metres only.

The reaction to the vibration of otter boards and rigging is minimal.

The escape from the disturbance centre is weak in the euphotic zone and very weak in the disphotic zone.

The escape is characterized by a momentary darting upward followed by an attempt to burrow into the bottom afterwards.

The maximum speed for escape reaches five times the length of the body per second.

The distance of the escape is relatively short, as fatigue appears after a distance 40 to 60 times the length of the body.

(ii) Group "B"

Biologic factors, among them mainly feeding, may be the cause of leaving the demersal zone.

Experiments show that types of this group react relatively strongly to changes in light intensity.

Types from this group may change their zone or become bunched together at the upper layers of the near bottom zone owing to the partial lack of oxygen at the bottom.

The reaction to vibrations of the ship's screw or other elements of the trawl gear is stronger than with group "A".

The reaction to the disturbance centres in the euphotic zone is stronger than in the disphotic layer.

The reflex action takes a direction according to the hydrodynamic characteristics of the body, usually downward.

The escape takes place from the disturbance centre, usually on a horizontal plane or downward. The maximum speed reaches six times the length of the body and tends to decrease with the size of individuals.

The distance of the escape is several times longer than with the representatives of group "A".

(iii) Group "C"

Fish from this group may change their living zone owing to biologic factors - like spawning at the bottom, feeding in various layers of the pelagic zone and in the demersal layer.

Physico-chemical factors may also influence the movement of types in this group. They strongly react to the intensity of light and oxygen content. Temperature and salinity may also limit their zone of living.

The fish from this group are very sensitive to the vibrations of the ship's screw and other elements of the trawlnet.

The reaction to visual stimuli in the euphotic zone is the strongest of all the ecologic groups, and this response suddenly weakens in the disphotic zone.

The direction of escape varies according to the hydrodynamic shape of the body.

The escape from the disturbance centre for the group "C" varies greatly, vertically as well as horizontally.

The maximum swimming speed is very high.

The ability to continue to escape till the first fatigue is great.

4 REQUIREMENTS TO BE MET BY TRAWLING GEAR

The material classified in this way may serve to show the requirements to be met by trawling gear destined to catch particular ecologic groups in their zone of living.

4.1 Characteristics required to catch bottom fish of ecologic group "A"

The trawling gear should adhere to the bottom.

The opening height of the trawlnet should not be so large as to seriously reduce the spread.

The trawling gear with its elements should cover the greatest possible area of ground.

The towing speed should be kept moderate.

Each of these characteristics is discussed hereafter:

4.1.1 Adherence to the ground This is mainly a matter of construction and rigging of the footrope. The footrope should have a suitable length and be suitably slackened relative to the headline. The adherence to the ground should be ensured along the whole length of the footrope.

4.1.2 Limitation of the opening height The efficiency of the gear when fishing for fish of group "A" is limited to the demersal layer which does not generally exceed 0.5 m. That is why the gear destined to catch such fish need not have a high ceiling but rather a broad and low (up to 1 m) opening.

4.1.3 Dragging the greatest area In order to fulfil its function the fishing gear must have the shape of a long winged net funnel. The wings in their working shape should be low and not exceed the height of the net opening. The wing spread should be the greatest possible and, estimated according to the length of the head-line, it should be 70 percent of the latter. The efficiency of such a gear may be increased by utilizing the "frightening" effect of the otter boards and bridles. They should extend the action of the wings in gathering the fish. For this close adherence of these elements to the ground has to be maintained.

4.1.4 Moderate towing speed The question of the most efficient towing speed should be considered from two aspects. Theoretically each increase of towing speed increases the area covered by the gear. On the other hand, excessive towing speed diminishes the shepherding effect of the elements of the trawling gear, as the speed of escape from the disturbance centres becomes less than the advancing speed of the gear. The towing speed should be adapted to the mean size of the fish, according to their maximum or near maximum swimming speed.

4.2 Characteristics required to catch fish in ecologic zone "b"

Although this group lives mainly in the demersal zone "b" under the influence of biotic or physico-chemical factors it may go into the pelagic zone "c", and fish of group "C" may enter zone "b", so we have to deal with a changing character of both these groups. This, in turn, increases the difficulty of generalising on the type of gear to introduce here. It seems necessary to consider the conditions of exploitation in zone "b" for both the ecologic groups "B" and "C". Fish from group "B" which temporarily pass into the pelagic zone will be dealt with in the next item. It must be decided if the exploitation of this zone should be carried out with the help of two different types of trawling gear. We shall try to do it by following the requirements imposed by the behaviour of the representatives of one and the other ecologic group.

4.2.1 Requirements for the exploitation of group "B"

The net must adhere to the bottom.

The opening height of the trawlnet depends on the type of fish concentration, mainly moderately high.

The net should preferably cover the greatest possible area of bottom.

The elements of the trawling gear can help to gather the fish.

Towing speed should be relatively fast.

These facts lead to the following principles in constructing the gear:

The wings should be relatively long - much longer than the length proposed for zone "a". The body of the net and the square should be a little bigger, owing to the towing speed and the swimming abilities of the group of fish. The footrope should adhere directly or by way of additional rigging to the bottom along the entire length. The opening width at greater towing speed and at a greater length of the wings should not exceed 60 per cent of the length of the headline.

4.3 Requirements for the exploitation of group "C"

The contact of the net to the bottom should be loose; digging of the footrope into the bottom is disadvantageous.

The opening height of the net should be as great as possible. This is connected with the opening width which should vary between 50 and 40 percent of the headline length.

The amount of catch depends more on the quantity of filtered water than on the bottom area dragged.

The towing speed depends mainly on the type of fish to be caught, and is of great importance.

As seen, most requirements are far from those given for group "B"; hence the typical gear for fish of the ecologic group "B" is not suitable in commercial fishing of pelagic fish temporarily living in the demersal zone "b". On the other hand trawlnets designed to catch pelagic fish in the demersal zone are well suited to catch fish of the ecologic group "B".

4.3.1 Characteristics for fishing in pelagic zone "c" In this zone in addition to the ecologic group "C" also group "B" (temporarily) may occur. Independently of the behaviour of fish from both these groups, the problem of the choice of shape and size of the trawl gear is easier than for zone "b". Here we do not have to deal with the bottom, which to some extent limits the escaping ability of any type of fish.

In the pelagic zone the direction of escape, reflexive as well as controlled and independent of the ecologic group, must be taken care of mainly by a suitable size of the net opening. This factor is even more important than the trawling speed, even when catching fast pelagic fish.

The opening size is also connected with the swimming speed of particular fish. It is not too important whether we consider sardine or sprat on one hand or mackerel or big herring on the other. If the size of the net opening was important when choosing the shape of the mouth of bottom or demersal nets, here it is decisive. It seems that we should fix approximately the value of the efficient action of the trawl in the pelagic zone, this action concerning the area of water masses covered by the trawl.

The shape given should be very similar to a circle, but in practice it is more or less the shape of a regular polygon (rectangle, square) which evolves in the farther parts of the body of the net into almost perfect circular shape.

The problem of the efficiency of the covered area is connected with two essential factors, namely: the swimming speed of the species caught and the trawling speed of the fishing gear. It seems that, with some approximation, we could determine the zero efficiency of a pelagic gear, taking as a base the observed response of particular types of fish to the gear. We already know a lot on this topic. For example, if it has been fixed that herring had reacted to disturbance of the environment by the gear at a distance of 4 m then the area of the opening of the trawl, in the case of a circular shape and with a zero efficiency of the trawl would be πr^2, in this case a little over 50 m^2. This area corresponds to the effective acting area of most bottom trawling gear. The wings or other elements preceding the opening of the trawl and which signal the arrival of the gear have a negative action in midwater trawls. The estimation of the opening area cannot be established automatically. As an example 100 m^2 give an opening radius of 5.65 m. If the band 4 m broad along the circumference of the opening is subtracted there remains a radius of hardly 1.65 m and this in turn gives an area of about 9 m^2 as effective opening area. To determine the required area it is necessary that the part of the radius corresponding to the planned area of efficient opening of the trawlnet be added to the opening radius of zero efficiency. In the example cited, the value corresponding to 50 m^2 is about 4 m, hence to get 50 m^2 of efficient area of the opening there must be a radius of nearly 8 m and so the line area of the opening will be about 200 m^2. This example illustrates in some way the necessities for effficient action of gear in zone "c". Undoubtedly the value of the supposed reaction distance is subject to discussion and the significance of this reaction may be diminished when increasing the trawling speed. This however has an influence on the filtration properties of the trawlnet, on the stronger action of the disturbance centres of the environment, etc.

This is undoubtedly confirmed by the good catch results even with a slow speed, when the opening is several hundred square meters and inversely the poor results with an increased trawling speed and a smaller opening. We seem to be right when fixing the lower limit of the opening size to 180 to 200 m^2 mouth area for commercial efficiency. Each increase of the opening area leads to an increase of the gear efficiency. Small fish like sprat or sardine require less of mouth area than bigger ones like mackerel. Speaking again of the problem of the size and the constructional proportions of the trawl gear in pelagic fishing, there can be dihedral or polyhedral constructions, though it is easier to get a circular opening when using a polyhedral construction than a dihedral one.

Greater trawling speeds may be obtained principally by increasing the filtering efficiency of the trawl, i.e. by elongating its filtrative part and having relatively big mesh at the initial part of the netting.

The problem of utilizing long or short wings, in principle, is only a way of getting a wide opening. Generally, it is possible to get it by relatively short wings.

The elements of the pelagic trawling gear should not cause additional noise or disturbance of the surroundings.

The trawling speed should be adapted to the species to be caught. Its increase, unless it diminishes the filtering efficiency and the opening area, is always an advantageous factor.

Due to the shorter wing length, the degree of the opening width must be considered differently from bottom or demersal trawlnets. It may reach even 70 percent of the length of headline or sidelines.

5 SELECTION OF THE SIZE AND SHAPE OF TRAWLING GEAR

The provisions given above may be of some help to a gear specialist who is able to take into account the requirements given. It is rather difficult to fix a priori definite size proportions for the particular elements of the trawl if the actual principles are derived from the character of exploitation or tradition.

The essential elements of the trawl and their interdependence are given below. See also Fig. 2.

Trawl mouth (a): Its area is determined by the encircling netting and base, by the perpendicular plane to the diameter of the trawl passing through the extreme points of the bosom.

Opening of the belly (b): As above, except that the plane passes through the bosom of the groundrope.

Body of the trawl (c): It is the element of the trawl between the bosom and the beginning of the codend proper.

Wings (d): The upper wings are an element of the trawl connected at the beginning with the square. The lower wings are an element connected with the first section of the belly.

Square (e): It is a netting element connected with the first section of the belly in the upper panel of the trawl.

Belly (f): It is the part of the trawl which forms a filtrative funnel (usually symmetric) beginning at the end of the square and running toward the codend, getting narrower.

Codend (g): This is connected with the belly and is characterised by an equal number of meshes in its circumference.

5.1 Trawls to be used for fish of group "A"

It is suggested to determine these general size proportions of the trawling gear which are used to catch bottom fish:

(i) The length of the upper wings is equal to the length of the body of the trawl

(ii) The width of the square, with meshes opened to half of their stretched length, is equal to the length of the body, or the length of the body of the trawl is equal to half the width of the square with its meshes stretched laterally

(iii) The length of the square varies within the limits of the maximum distance that the fish of this ecologic group perceive or feel the frightening action of the fishing gear

(iv) The length of the codend proper depends on the yield of the fishing ground and the technique used in fishing

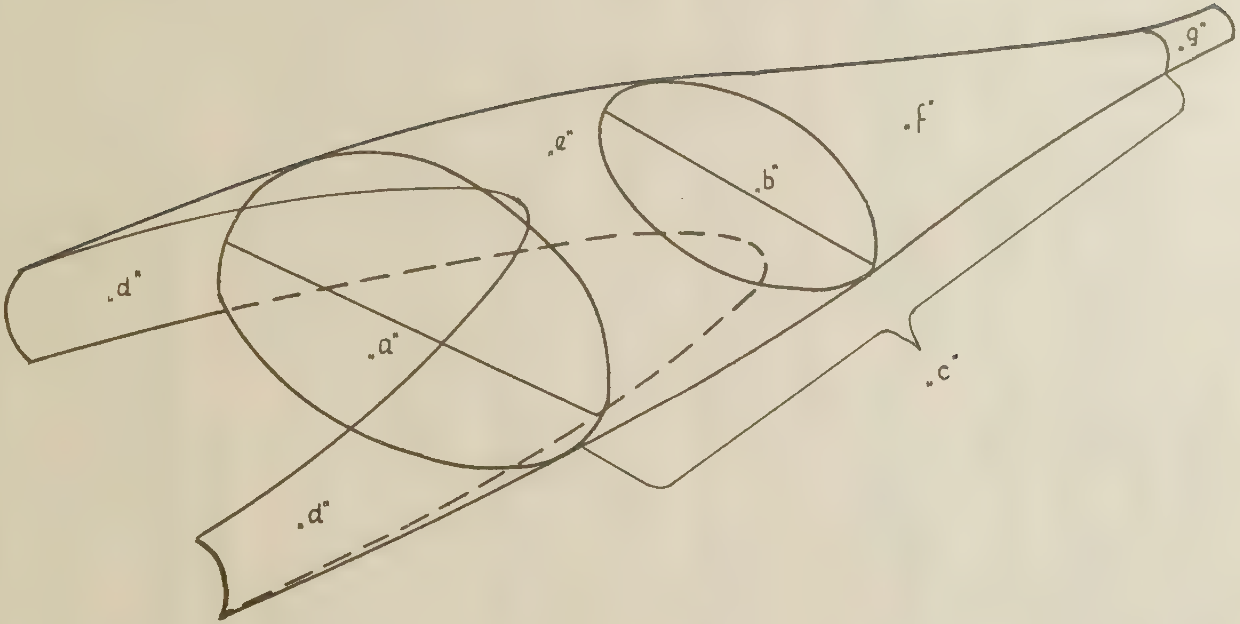

Fig. 2 The shape of the trawlnet and its elements

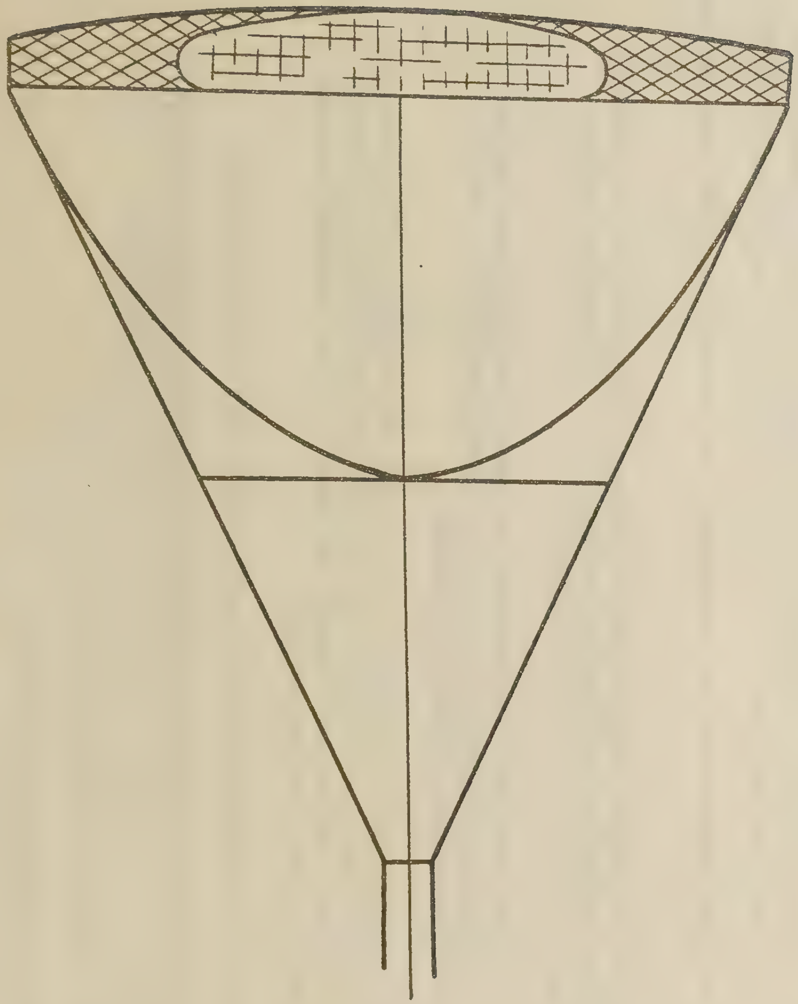

Fig. 3 Upper and front view of the proportions of the trawlnet designed for the exploitation of zone "a"

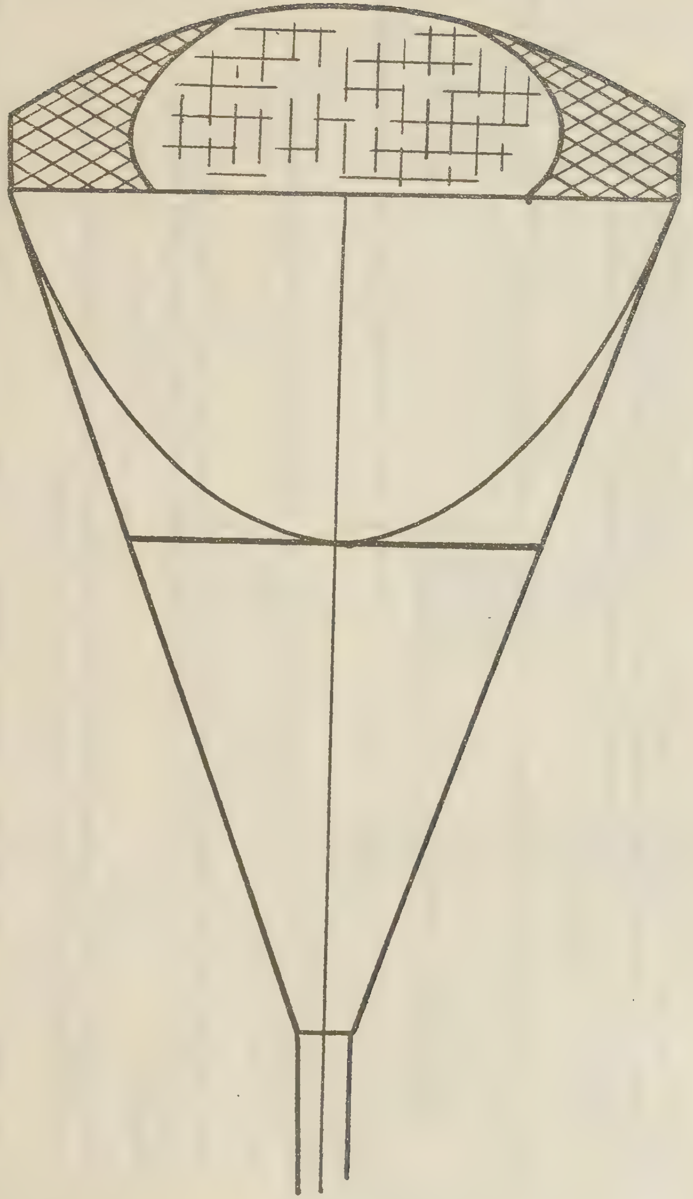

Fig. 4 Upper and front view of the proportions of the trawlnet designed for the exploitation of fish from group "B" in zone "b"

(v) The construction of the wings should be low at the winglines; in the further parts near the square, the form of the headline and of the groundrope and the horizontal distance between the doors should be taken into consideration

Figure 3 illustrates the shape and the size proportions of the trawlnet destined to fish in zone "a".

5.2 Trawls to be used for fish in zone "b"

A) Suggestions for the construction of trawlnets for catching fish of the ecologic group "B":

(i) The length of the upper wings is equal to the width of the square when in action or half this width, stretched

(ii) The length of the body is equal to 62.5 percent of the width of the square stretched or 125 percent of the width of the square (with open meshes)

(iii) The length of the square should not be less than the distance of perception or feeling of the fishing gear by fishes

(iv) The length of the codend proper depends on the yield and deck handling

(v) The width of the upper and lower wings is already greater than in the typical bottom gear. This ensures a sufficiently large opening of the trawl at the base

(vi) The shape of the opening of the mouth at the level of the square should be that of a flattened ellipse. The drawing shows the given proportions

B) Suggestions for the construction of trawlnets for catching fish of the ecologic group "C":

(i) The length of the upper wings does not exceed 75 percent of the width of the square in action or else it is equal to 37.5 percent of the width of the square with stretched meshes

(ii) The length of the body of the trawlnet is equal to 75 percent of the width of the square stretched or else 1.5 times longer than the dimensions of the square with open meshes

(iii) The length of the square depends on the size, especially on the opening height. If the ceiling is high the square does not need to be moved forward. If not, the height should be equal to the maximum distance of perception of the species sought

(iv) The length of the codend depends on the yield and deck handling

(v) A great part of the wing width, mainly for the upperwings, begins at the winglines

(vi) The shape of the opening should be that of an arc

Figure 5 shows the above proportions.

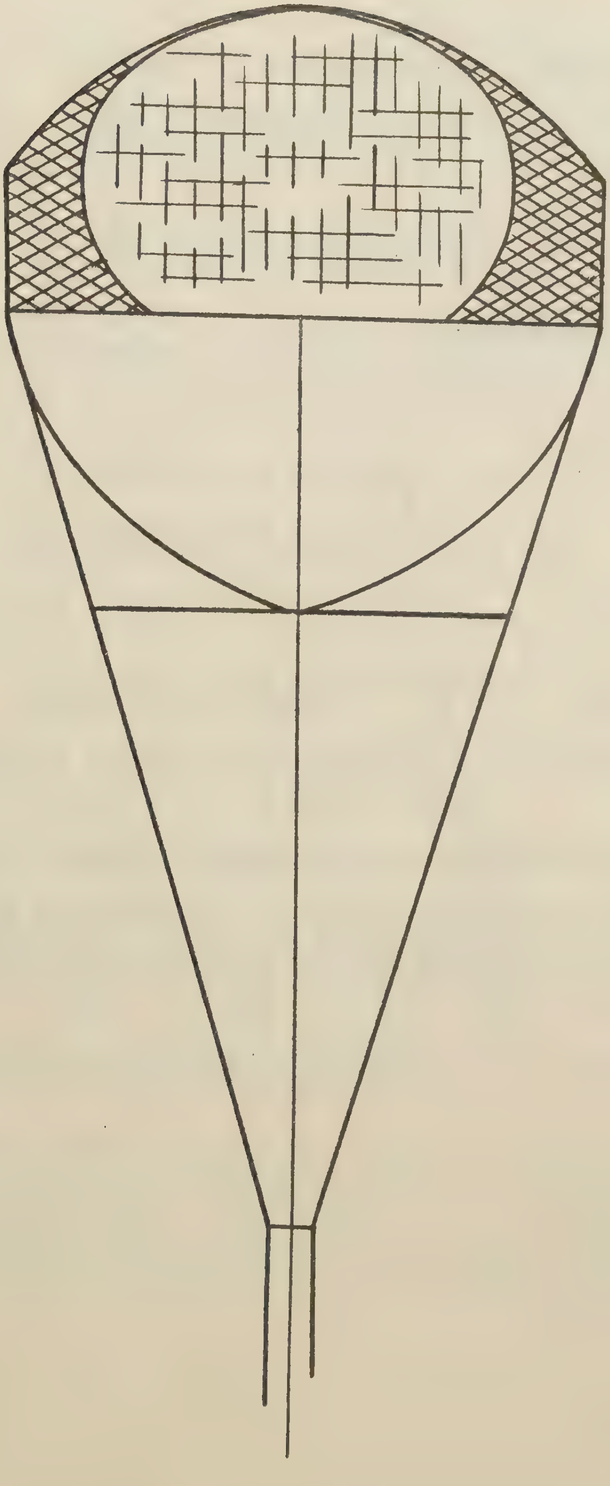

Fig. 5 Upper and front view of the proportions of the trawlnet designed for the exploitation of fish from group "C" in zone "b"

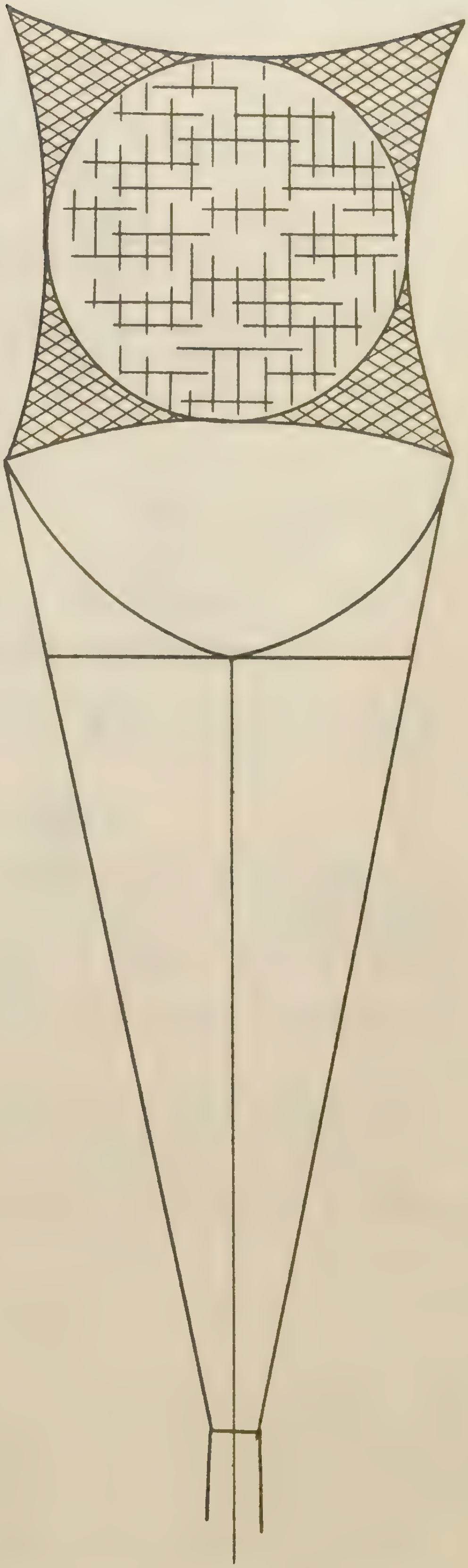

Fig. 6 Upper and front view of the trawlnet designed for the exploitation of fish in zone "c"

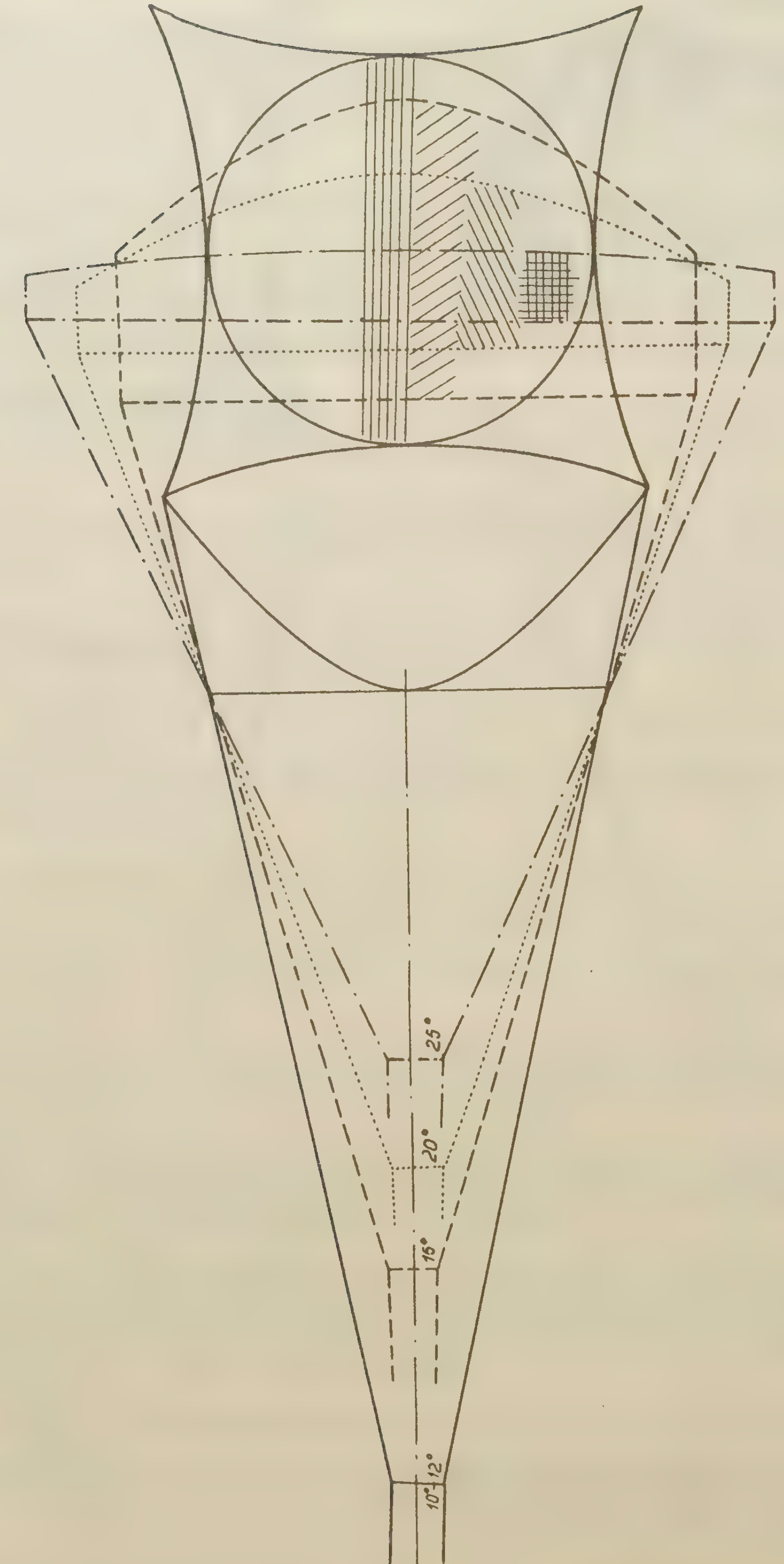
25°
20°
15°
12°
10°

Fig. 7 Compound view based on a common diametral and the perpendicular

5.3 Trawls to be used for fish in zone "c"

The following suggestions are given for the construction of trawlnets used for catches in zone "c" (pelagic zone). These suggestions are based on the requirements dealt with previously and on the discussions held on this matter.

(i) The length of the wings is about 50 percent of the width at the bosom when in action, i.e. 25 percent in its stretched form

(ii) The length of the body depends mainly on the opening size and in tetrahedral constructions it should be 2 to 2½ times the width of the first panel of the body when in action or at least equal to the width of this panel when stretched

(iii) The trawlnet has no square

(iv) The opening area is of a circular or a polygonal shape where the height and width are approximately the same

(v) The length of the codend depends on the yield and deck handling

(vi) The towing speed should be faster than the swimming capabilities of the fish to be caught

Figure 6 shows the proportions of the trawlnet used in the pelagic zone for the fish of the group "C" as well as "B".

5.4 General remarks concerning the shape of the trawlnets

The selection of the length of the trawl body and the selection of the width of the wings in all the types presented here is derived from the angle of attack of the netting in regard to the opening height of the trawlnet. This is illustrated in Fig.7 where the angle of attack of the netting is compared with the diameter of the trawlnets.

As shown, the horizontal angles of attack vary from 25° in typical bottom trawlnets to 12° to 10° in pelagic trawlnets.

The vertical angles of attack of the netting, in regard to the vertical opening, are as follows: in typically bottom trawlnets this angle is very small (about 1°); in trawlnets for the demersal zone it is about 5° and for pelagic fish of this zone it is 10°; finally in pelagic trawlnets it is 10° to 12°. We have here the opposite tendency to he horizontal, i.e. the angles increase as the body of the trawl elongates.

* * * * * * *

BEHAVIOUR OF HAKE (MERLUCCIUS MERLUCCIUS L.) IN RELATION TO TRAWLS WITH WIRE CABLE BRIDLES

by

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Abstract

In the Adriatic Sea, Yugoslav and Italian fishermen wrap their wire trawl bridles with manila rope of about 300 m length, in the belief that the thicker the cable the greater will be the catch. To test this hypothesis, comparative fishing experiments were made with special attention to the behaviour of hake in relation to fishing techniques.

These experiments showed that, contrary to expectation, the average lengths of hake were in fact greater when an uncovered bridle was used. This kind of bridle also seemed to increase the selectivity of the gear.

E/14

COMPORTEMENT DU MERLU (MERLUCCIUS MERLUCCIUS L.) DEVANT DES CHALUTS AUX BRAS EN CABLE METALLIQUE

Résumé

Dans l'adriatique, les pêcheurs yougoslaves et italiens entourent le câble métallique des bras de leurs chaluts d'environ 300 mètres de corde de manille, dans la conviction que plus les bras sont épais et plus l'engin prend de poisson. Pour vérifier cette hypothèse, des pêches comparatives ont été effectuées en s'attachant particulièrement au comportement du merlu par rapport aux diverses techniques employées.

Les essais ont révélé que, contre toute attente, la taille moyenne des merlus ramenés par le chalut était plus grande lorsque les bras étaient nus. Ce type de gréement paraît aussi accroître la sélectivité de l'engin.

COMPORTAMIENTO DE LA MERLUZA (MERLUCCIUS MERLUCCIUS L.) CON RESPECTO A ARTES DE ARRASTRE CON MALLETAS DE CABLE DE ACERO

Extracto

En el Mar Adriático, los pescadores yugoslavos e italianos forran sus malletas con cabo de abacá de unos 300 metros de longitud porque suponen que cuanto más gruesa es la malleta mayor será la captura. Para comprobar la validez de esta hipótesis, se hicieron experimentos de pesca comparativa prestándose especial atención al comportamiento de la merluza con respecto a las técnicas de pesca.

Los experimentos demostraron que, por el contrario de lo que se suponía, las tallas medias de la merluza eran mayores cuando se empleaban malletas sin forrar. Esta clase de malleta también parecía incrementar la selectividad del arte.

1 EXPERIMENTAL DESIGN

Comparative fishing experiments were made during cruises of the R/V Bios, south of Cape Ploče, on the lines 43° 22.0'N, 15° 53'E to 43° 15.6'N, 15° 55.6'E, from 14 to 19 June 1956 (24 hauls); 21 to 23 October 1956 and 25 to 28 November 1956 (12 + 12 hauls); 1 to 6 February 1957 (24 hauls) and from 13 to 23 April 1957 (24 hauls). A total of 96 hauls were made, 48 of them with uncovered wire cable bridle (w) and 48 with wire cable bridle covered with manila (m). The gear and mode of operation were unchanged throughout the experiments. Each day four standard hauls, each of one hour duration, two with uncovered bridle and two with manila covered bridle, were made at random over the same area, marked with buoys (Županović and Grubisić, 1958; Županović, 1963).

2 SPECIFICATION OF GEAR

The dimensions of the locally produced cotton nets were: wing height 170 meshes (mesh size 55 mm), headline length 18 m, groundrope length 22 m, total length of net 46 m and the codend of mesh size 22 mm enveloped in a loose cover of 40 mm mesh netting. In the experiments either an 11 mm thick wire cable bridle, of 100 m length, or a 40 mm thick cable bridle of 120 m length bound with manila, was used. The length of the towing warps was 450 m.

3 RESULTS

The catches of hake in the experiments with wire cable bridle showed considerable fluctuations from day to day and from season to season. Larger catches were obtained in the early morning hours and smaller catches by day. The largest catch per unit of effort for one hour's haul was registered in summer. Also, the greatest number of mature males and females was caught in summer. The catch per unit effort varied from 3.45 to 16.05 kg. The maximum number in the catches was 104 fish and the minimum was 43. The length range was 4 to 83 cm. The average length of fish in all the catches combined was 23.97 cm.

In October and November the number of hake taken with the uncovered bridle decreased considerably, probably due to the migration of small and medium sized hake to shallower waters in autumn (unpublished data). The maximum number of individuals in one hour's haul was 44, the minimum 8. The maximum weight of catch per hour was 8.15 kg and the minimum 1.55 kg. The length range was 6 to 85 cm. The average length of fish caught by the two methods of fishing was 25.15 cm.

In February the number of adult individuals in the catches decreased. Due to the low temperatures in the shallower waters adult individuals probably migrate into deeper waters. The average length of hake, caught in February, by the two methods of fishing was 22.27 cm. The maximum number of fish in a catch was 64 and the minimum 8. The maximum weight of the catch per unit effort was 5.90 kg, and the minimum 1.40 kg. The length range of fish was 5 to 63 cm.

In April the number of adult individuals in the catches again showed a tendency to increase. The average length of hake caught by both methods was 24.54 cm. The maximum weight of catch was 8.20 kg, and the minimum 1.08 kg. The maximum number of fish in a catch was 42 and the minimum 9. The length range was 6 to 57 cm.

4 SELECTIVITY

The following statement summarises the differences found between the catches of hake using covered and uncovered bridles.

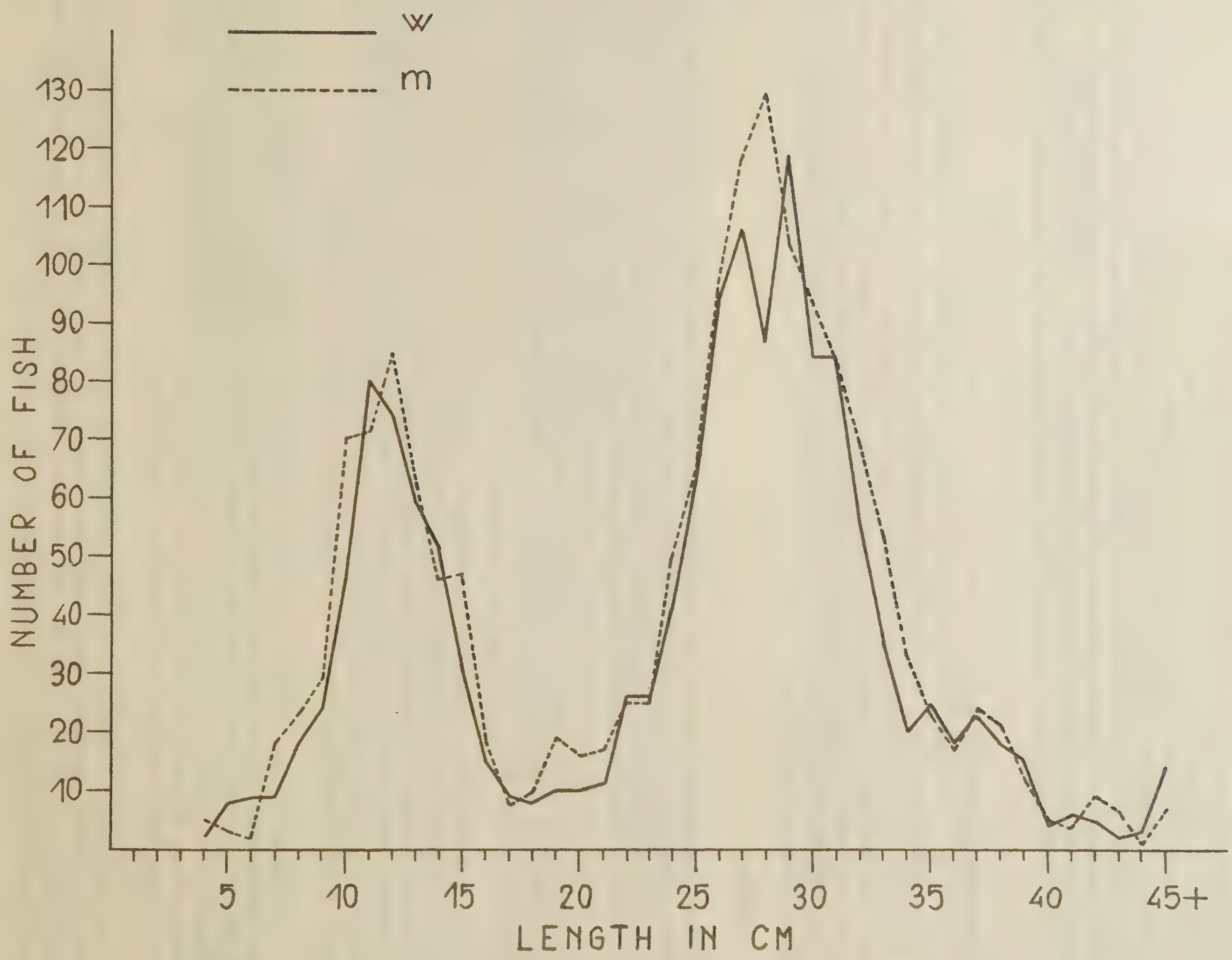

Fig. 1 Length frequency of hake in the catches with wire cable bridle (w) and with wire cable bridle covered with manila (m)

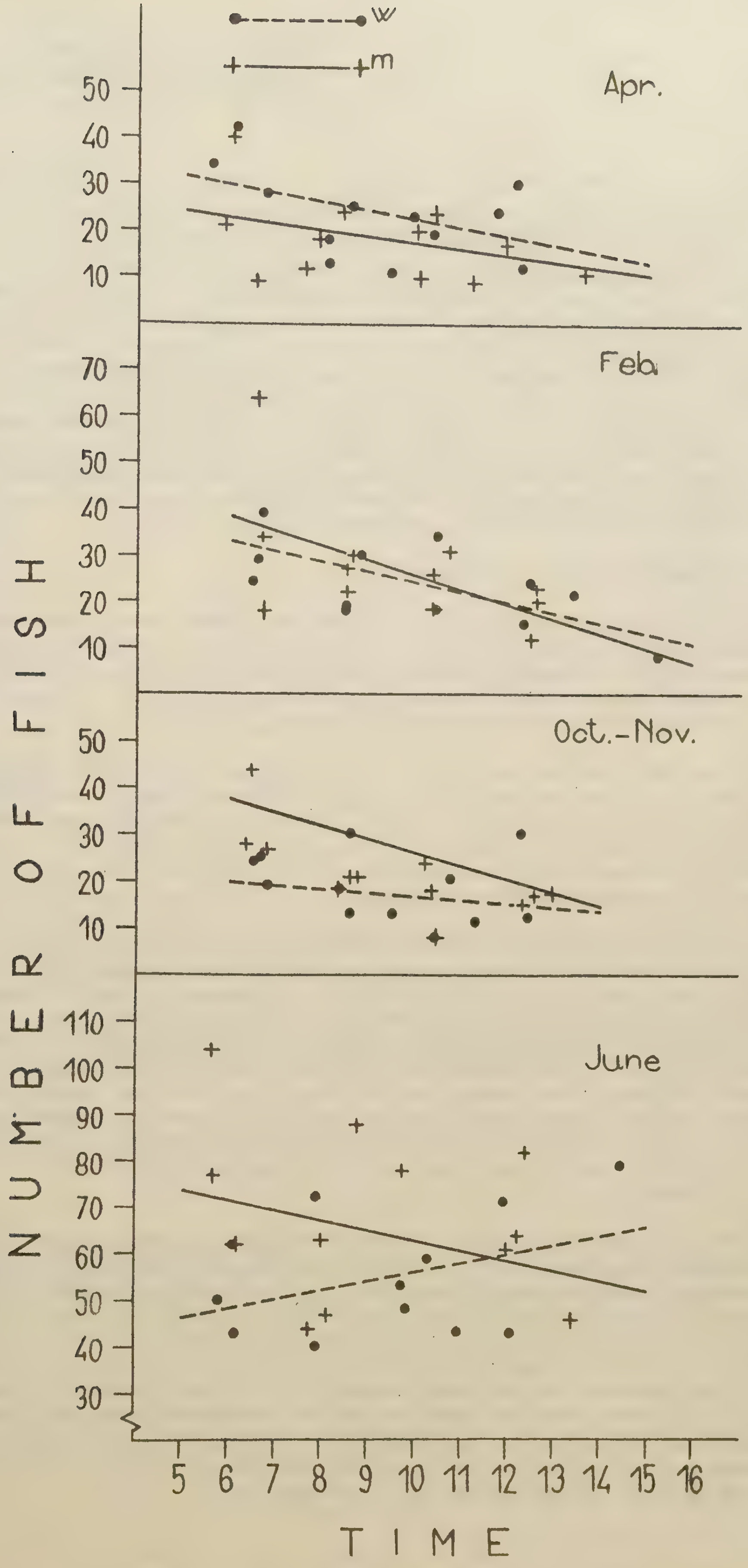

Fig. 2 Diurnal changes in catches of hake with wire cable bridle (w) and with wire cable bridle covered with manila (m) in relation to daily light changes at

	Weight difference %	Numerical difference %
Experiment 1	5.06	10.34
Experiment 2	5.72	8.94
Experiment 3	0.40	7.60
Experiment 4	11.04 (-)	13.30 (-)
Total	1.78	5.76

It is evident that the numerical differences are larger than the weight differences. The average length of fish, which is an important economic factor in commercial fishing, was greater when an uncovered bridle was used than when the manila covered bridle was operated (with the exception of the fourth experiment). The variations in length values of hake are shown in Fig. 1.

5 DIURNAL CHANGES IN THE CATCHES OF HAKE

Diurnal and seasonal migrations of hake can affect the catch considerably. Diurnal changes in the number of hake are often followed by corresponding changes in their size composition. Hickling (1933) stated that in catches of hake off Ireland smaller fish showed the greatest diurnal fluctuations and that diurnal variations in the catch decrease with increase in size of fish.

Variations in size composition have been evident, not only between night and day but also within different periods of day. Woodhead (1964), analysing the trawl catches in the North Sea from dawn to dusk, showed that the average lengths of both whiting and haddock tended to increase during each day's trawling. The greatest number of small fish was caught in the first haul after sunrise while the largest fish were obtained in the catches at dusk.

Diurnal variations in catch in the experiments with wire cable bridles might also be related to the behaviour of hake in response to the gear used. The results of experiments performed during daylight hours in summer, autumn, winter and spring periods were analysed and the diurnal changes in the catches of hake are shown in Fig. 2. From the data presented it is seen that the largest catches were obtained mainly in the first haul after sunrise. The only exception was the catch obtained by using uncovered bridle in the summer period, when the greatest number of mature males and females was caught (unpublished information). Changes in physiological conditions probably brought about this variation in the pattern of diurnal appearance of hake in the catches. In the other seasons the diurnal changes in the catches do not show essential variations.

In all the seasons there is a gradual decrease in the number of hake caught, as the day progresses. This might be due to the changes in light intensity and the visual reactions of hake to bright daylight. This is in conformity with the results of observations made by Blaxter, Parrish and Dickson (1964) in tanks and at sea, that vision is the most important factor in determining the behaviour of fish in relation to fishing gear. But the visual capabilities of hake appear to be better expressed in the catches using bridles without manila covering. This is seen in the greater average lengths of hake in these catches which might be associated with the greater transparency of the sea water and the greater possibility of escape of smaller fish through the meshes of the net especially its front part. This is probably the reason for the relatively less number of small fish in these catches.

6 OTHER OBSERVATIONS

A covered bridle (particularly if it be a long and thick one) changes the transparency of water masses during the trawl and this may be expected to affect diurnal changes in the catch of the smaller hake. By examining the relation between the catches of hake and the mean extinction coefficient of haul in the Channel region of the Middle Adriatic in 1957/1958, it was found that an interrelationship existed between these phenomena. A total of 126 hauls were made, each of one hour duration, with simultaneous observations on the transparency of the sea water by Secchi disc. The results obtained are given in Fig. 3. The observed regression was found to be highly significant ($P/t < 0.01$).

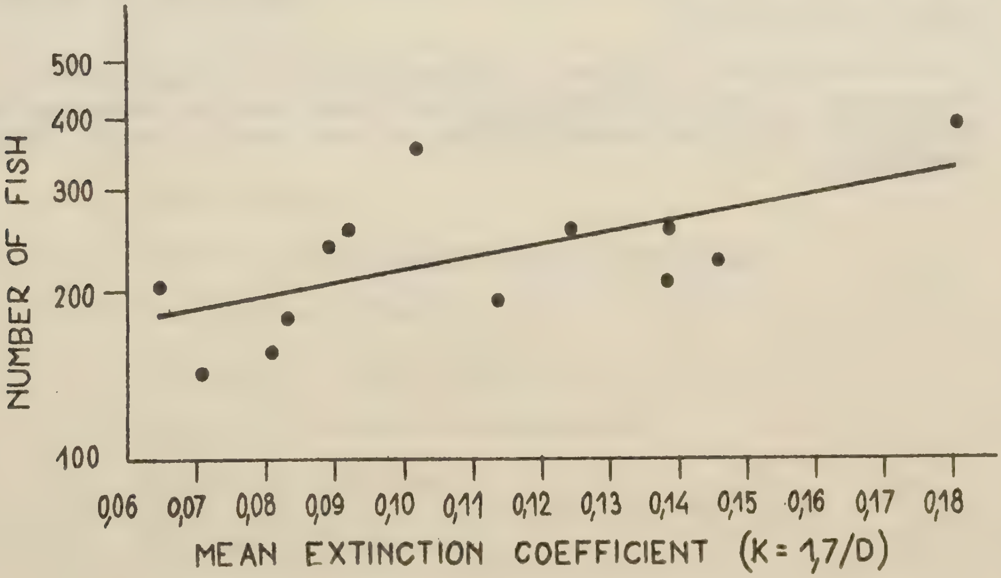

Fig. 3 Catches of hake in relation to mean transparency of haul in the Channel region of the Middle Adriatic during the period July 1957 to July 1958

7 CONCLUSION

The average lengths of hake caught in the fishing experiments were greater when wire cable bridles without manila covering were used. The diurnal variations in the number of hake caught were accompanied by corresponding variations in their size composition which were evident not only from day to day but also from season to season.

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SOME ASPECTS OF THE REACTIVITY OF FISH TO VISUAL STIMULI IN THE NATURAL AND IN A CONTROLLED ENVIRONMENT

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Abstract

Several behaviour patterns of fish that are of interest to fishing gear and tactics depend, at least in part, on vision. Recent data about the hierarchical ways in which sensory information is processed in the neural structures and then leads to behaviour, indicate that we run the risk of overestimating the level of integration and thus of misinterpreting the biological consequences of the activities an animal shows under simplified artificial stimulus conditions. With regard to vision, it seems essential to take into full account the recent findings about the angular radiance distribution in the fish habitat. This seems of importance with regard to the neural processing of visual information. Examples are given of the reactions of fish under simplified visual stimulus conditions.

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CERTAINS ASPECTS DE LA REPONSE DES POISSONS AUX STIMULI VISUELS DANS LEUR MILIEU NATUREL ET DANS UN MILIEU CONTROLE

Résumé

Nombre de comportements du poisson présentant un intérêt pour les engins et les tactiques de pêche dépendent, du moins en partie, de la vision. D'après des données récentes sur la "hiérarchisation" du traitement que subit l'information sensorielle dans les structures neurales avant de se traduire en comportement, il existe un risque de surestimer le niveau d'intégration et, partant, de mal interpréter les conséquences biologiques de l'activité que manifeste un animal dans des conditions artificielles, devant des stimuli simplifiés. Pour ce qui est de la vision, il semble indispensable de tenir pleinement compte des récentes découvertes sur la distribution angulaire des rayonnements dans l'habitat du poisson. Ce point paraît présenter de l'importance pour ce qui est du traitement neural de l'information visuelle. L'auteur fournit des exemples de réactions du poisson à des stimuli visuels simplifiés.

ASPECTOS DE LAS RELACIONES DE LOS PECES ANTE ESTIMULOS VISUALES EN AMBIENTES NATURALES Y ARTIFICIALES

Extracto

Varias modalidades del comportamiento de peces, que interesan en lo relativo a los artes y métodos de pesca, dependen, por lo menos en parte, de la vista. Datos recientes sobre las maneras en que la información sensorial se interpreta en las estructuras neurales y da por resultado el comportamiento, indican que existe el peligro de exagerar el nivel de la integración y, por tanto, de interpretar erróneamente las consecuencias biológicas de las actividades de un animal en condiciones estimuladas simplificadas y artificiales. Con respecto a la vista, parece ser esencial tomar nuevamente en consideración los recientes resultados obtenidos sobre la distribución del flujo radiante angular en el habitat de los peces. Esto también parece revestir importancia con respecto a las reacciones neurales de la información visual. Se dan ejemplos de las reacciones de los peces ante estímulos visuales simplificados.

1 INTRODUCTION

Some of the behaviour patterns of fish that, at least in part, depend on vision and that are of interest with respect to fishing gear and tactics, are:

a) the diurnal activity pattern

b) the diurnal vertical migration

c) schooling

d) the avoidance of nets

e) the concentration around stationary objects

f) the concentration around an artificial light source

It is not the object of this paper to give extensive reviews of the literature on these behaviour patterns. Several authors have given such reviews on various occasions. During this conference other papers will devote special attention to some of these behaviour patterns. The purpose of this paper is to point to some neglected aspects and to some gaps in our knowledge with respect to both the visual stimulus field under water and the resulting behaviour patterns in fish.

These shortcomings hinder our efforts to improve upon trial and error in developing new fishing gears and tactics by deliberate and purposeful designing. The development of new gears and tactics cannot, of course, be postponed until we understand all about visual stimulus fields and fish behaviour. Therefore trial and error approaches will continue to yield valuable contributions to the improvement of gears and tactics.

2 NATURAL AND CONTROLLED VISUAL ENVIRONMENT

In the outline of subjects for this conference the natural environment of the fish was distinguished from the controlled environment. Fishing could, however, be considered as controlling the natural environment of the fish so as to induce them to concentrate at a suitable place from where they can be removed from the water with minimal effort. Conversely, for studying "normal" fish behaviour in the laboratory, the ideal controlled environment should closely imitate the natural environment. Obviously we should first have a detailed knowledge of

a) the normal visual environment of the fish

b) its visual faculties

c) its behaviour as depending on (a) and (b)

Secondly we should know how the fish behaviour will deviate or be disordered through changes introduced into its normal visual environment.

From the many attempts to reduce the complex orientational behaviour patterns of animals in natural light fields to more simple responses, such as photokinesis and phototaxis under laboratory conditions (Fraenkel, Gunn, 1961), one might get the impression that the "intensity" and the "direction" of the "light" are appropriate parameters for qualifying and quantifying a light field. The intensity seems to be related to concepts such as kinesis and preferendum, the direction of the light to the taxis concepts.

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Both from a physical and a behavioural point of view, serious objections must be raised against this situation. From a physical point of view intensity (leaving aside which intensity) and direction might each only be considered as a useful parameter for light fields that meet quite definite requirements: a light field should be completely diffuse for intensity to be a parameter, while direction asks for a parallel shaft. These two types of light fields are, however, not found in nature and they are, moreover, extremely difficult to produce under controlled conditions, especially under water. Theoretically (Preisendorfer, 1959) these two types of light fields - the diffuse field and the parallel shaft - are the limiting shapes to which the natural light field produced under water by both scattering and absorption, is shifted when respectively either scattering or absorption alone effects the light field (if the water is assumed to extend unlimited, reflection can be left out of consideration).

It must be assumed that the visual information releasing and steering behaviour patterns in fish is derived from the local and momentary flux distribution under water. Arguments have been presented for assuming that, for natural behaviour to occur, the fish must be able to sample visual information from a more or less natural flux distribution(Verheijen, 1958). The behaviour of fish is disordered in complicated ways as soon as an experimental light field approaches to some extent either a diffuse field or a parallel shaft.

3 THE CONCEPT OF BEHAVIOUR

In this connection, the concept of behaviour must be more closely examined in relation to recently emerging insight into the ways in which sensory information is being coded and processed and is governing behaviour. The concept of behaviour has been subjected to several attempts to arrive at a definition. According to Tinbergen (1951) behaviour is the "total of movements made by the intact animal". Similarly Barnett (1962) defines behaviour as "the whole of the activities of the animal's effector organs". In general the behaviour in the habitat must be assumed to be adaptive in that it contributes to the animal's chances of survival or reproduction (see for instance Tinbergen, 1951, 1963; Scott, 1958; Hinde, 1966). As touched on above, it is doubtful whether the activities of an animal under controlled conditions will always meet these requirements. In general the "disordered" character of such activities has not been recognized, and this leads to misinterpretations when they are applied as a basis for understanding behaviour in the habitat.

The hierarchical character of the organization of behaviour has long been recognized (for discussions see, for instance, Tinbergen, 1951, 1963; Baerends, 1958; Hinde, 1966). It seems justified to label behaviour as "natural" when it leads to biologically adaptive consequences. In the hierarchical organization of such a behaviour pattern, the goal-directed character is found again at several levels of integration, from the simplest reflex up to more complex levels. In nature, the external and internal situation of a given organism determines at any time up to which level integration must proceed in order to lend survival value to its behaviour.

Experimental evidence that will give a more detailed insight into the nature of the hierarchical organization of behaviour will be derived from:

a) studies of behaviour patterns produced by electrical stimulation of the central nervous system

b) electrophysiological studies of the ways in which different parameters of a stimulus situation are analyzed and coded in the sense organs and in the sensory pathways up to the central nervous system.

Both types of experiments have been performed in evertebrates and in vertebrates but fish have hardly ever been used. However, some basic rules seem to govern the hierarchical handling of sensory information and the hierarchical releasing of behaviour patterns in widely divergent species of animals.

4 HIERARCHY IN MOTOR INTEGRATION

Electrical stimulation of localized parts in the optic tectum of the trout (Salmo irideus) induced coordinated movements of the eyes (visual grasp reflex), the body, the fins, and, with strong stimulation, the mouth, which would normally have been performed when a prey had been perceived somewhere in the periphery of the visual field (Akert, 1949a, 1949b). Similar feeding behaviour and other types of behaviour - from simple ones (eye movements) to most complicate patterns (attack, flight, going to sleep, etc.) have been elicited in other animals. In some cases the animal performs only stereotyped movements as if it were a machine, while in other instances the behaviour of the stimulated animal cannot be distinguished from the complicated and subtle movements the animal will show when normally motivated under adequate stimulus conditions. Among the numerous experiments, those of von Holst and von Saint Paul (1963) are of particular importance for our purpose. These authors studied the results of intracranial electrical stimulation in fowl. A complex chain of behaviour patterns could result from stimulation with gradually increasing strength by an electrode in a given position. Some characteristics of such a chain of behaviour patterns are that the activities, which together form the chain, always appear successively in the same sequence and that this sequence is a natural one having a clear biological consequence. More simple activities out of the chain could be elicited separately by electrodes at different intracranial locations but then the performance had a "meaningless" mechanical character. Such relatively simple activities like sitting down, scolding and pecking could each also appear as a component integrated in very different chains of behaviour. Some complicated chains could be performed in a complete and quite "natural" way as a result of intracranial stimulation in the absence of an adequate external stimulus situation (cf. vacuum activity). Other patterns, for instance fighting, called for an object with definite characteristics with respect to appearance and reactivity, towards which the behaviour could be directed. Therefore the authors emphasized that, when trying to identify a centrally evoked activity, we run the serious risk of under-estimating the level of integration of the behaviour that can potentially be released by the neural structures at the location of the electrode, because, if a more adequate external stimulus situation had been present, a more complete and complicated chain of activities might have resulted from the central stimulation at the chosen location.

At this point we arrive at the principal and suggestive thesis of this paper: we reversely run the risk of over-estimating the level of integration and, inevitably, of misinterpreting the biological consequences of the activities an animal shows "spontaneously" under controlled, and therefore generally artificial, stimulus conditions. In order to arrive at the arguments for this thesis, attention must be asked for recent findings with regard to the coding of sensory information.

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5 HIERARCHY IN SENSORY INTEGRATION

Studies of the electrical activity of units in the pathway from receptor cell on to the central nervous system have revealed that a given ganglion cell will be activated only by a stimulus with a particular spatial and temporal configuration. Although similar rules have been found in receptor systems for touch, sound and electricity, we shall confine our considerations to the visual system and only a few papers out of the recent elaborate literature will be mentioned. By using a variety of light sources and visual targets (stationary and moving spots, contrasts, stripes and more sophisticated stimulus situations) one has demonstrated that in crustaceans (Waterman, Wiersma, 1963), in the frog (Maturana, et al., 1960), in the pigeon (Maturana, Frenk, 1963), in the rabbit (Barlow, et al., 1964; Levick, 1967) and in the cat (Hubel, Wiesel, 1962; Baumgartner, et al., 1964) progressively both a temporal and a spatial integration of information, produced by the stimulation of the receptor cells, takes place along the visual pathway up into the sensory centres. In this way, different aspects of the retinal stimulus situation, from rather simple to most complicated with regard to stimulus intensity, extensiveness, contrast, form, movement, etc., become available to the animal in parallel channels. There are, moreover, indications that ganglion cells selecting one or more special parameters out of the original stimulus situation are able to do so by means of the shapes and sizes of their dendritic field, because this secures a particular pattern of connection with the afferent cell pools (see, for instance, Maturana, et al., 1960; Young, 1964), although the selectivity might also be based upon functional selective capacities of the cells independently of specific afferent pathways (Maturana, Frenk, 1963). There is, moreover, histological and electrophysiological evidence that, in some vertebrates, the ganglion cells that detect special parameters of the original stimulus complex are grouped together in parts of the central nervous system in sheets which cover each other topographically in a way that might be compared with a pile of maps of a given country, each map locally indicating a particular aspect such as population density, type of soil, agriculture etc. Thus, when we penetrate the pile in a vertical direction, we successively encounter the different parameters which together completely describe the situation at the chosen locality (Maturana, et al., 1960, optic tectum frog; Hamdi, Whitteridge, 1954, optic tectum pigeon; Hubel, Wiesel, 1963, striate cortex cat). It is not unlikely that detectors attuned to simple parameters, such as contrasts, and sampling this information at an early stage of coding and processing the sensory input in the visual pathway, are related to the release of simple activities at a low level of integration, for instance, the above described visual grasp reflex. This seems to be one of the first activities of the orientation reaction (recently extensively studied by Russian and other workers, see Lynn, 1966). At a higher level of integration detectors attuned to more sophisticated aspects of the stimulus situation must be assumed to deliver information to the neural structures involved in the release of more complex behaviour patterns to be performed by the animal as a functional unit, such as described above in fowl.

With the above suggestive data about the hierarchy in sensory and motor integration in view, it seems sensible to imagine that the following processes take place in succession as soon as a visual stimulus appears in the animal's habitat: detectors attuned to relatively simple parameters, such as contrast, start the orientation reaction with eye movements (visual grasp reflex) in the direction of the contrast-producing stimulus situation. In order to decide whether, after this "approach by the eye", the animal as a functional unit has to perform either approach or withdrawal (Schneirla,1965), detectors at increasingly higher levels of sensory information with increasingly more complicated receptive fields deliver step by step information about other and more complicated spatio-temporal configurations of the stimulus situation. When the information sampled at higher and higher levels of integration meets certain requirements ("sign-stimuli") higher and higher levels of integration are drawn into action, so that finally the animal as a functional unit performs either approach or withdrawal as an adaptive pattern of behaviour. Under stimulus conditions characteristic for the animal's habitat, low level activities such as the visual grasp reflex (eye or head movements) are performed a fairly large number of times with regard to several types of contrast producing stimuli before a stimulus situation is encountered, which in addition, produces information releasing activity at higher levels of integration; now approach or withdrawal, integrated in an appropriate behaviour pattern, and performed by the animal as a biologically functioning unit, appears.

The picture given above of neural activity proceeding from low to high levels of integration might seem contradictory to the usual conception that lower levels are controlled by higher levels but this is only a seeming contradiction. This is not the place to discuss this point further.

6 DISORDERED BEHAVIOUR

Behaviour of the biologically non-adaptive stereotyped low-level type as produced by electrical stimulation of the central nervous system may in vertebrates appear also after damage to parts of the central nervous system. The damage may be caused by surgical interference in animals (the Klüver-Bucy syndrome) or by disease in the human being (dissolution of the central nervous system in the Jacksonian sense; for a confrontation of data and theories from ethology, psychology and psychiatry, see Ploog, 1964). Obviously the damaged or separated nervous structures are no longer able to play their part in handling the high-level sensory information. In an arbitrary stimulus situation they fail to produce the decision that the orientation reaction with regard to some contrast has to be restricted to the eyes, for instance, so that "approach" activity spreads over more and more motor centres, with the result that ultimately the organism as a whole - let along the defective neural structures - performs approach in a stereotyped "forced" manner. A superficial observer might, for instance, be of the opinion that the patient or the animal tries to eat an object in its environment. This, however, would be an overestimation of the level of integration: the unnatural non-adaptive character of the behaviour appears when inedible or even dangerous objects are treated in the same way, even after an immediately preceding bad experience. Of the human being, a monkey or a cat we can relatively easily recognize the behaviour pattern "approaching an object and trying to eat it" and we know whether the object is suitable or not for this purpose and, if not, we conclude that something is wrong.

When studying fish and behaviour patterns such as those mentioned in the beginning, anthromorphizing is less likely to indicate intuitively whether the animal behaves natural or not or even what the animal does at all. Originally students of animal behaviour started by observing the animal in its natural habitat. More recently there is an increasing tendency to place the animal in a rigidly controlled environment and, when the animal is studied in its habitat, to measure environmental parameters that are assumed to be relevant. Restricting our further consideration to fish and to its visual environment, we have to realize what types of controlled environments are used and should be used and which environmental parameters are measured and should be measured.

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In the laboratory, the typical controlled environment for a fish is a rectangular or circular tank with white, grey or black walls and with nothing to be seen in it except the stimulus to be studied. Examples are: the lamp or lamps producing the "intensity" or the "gradient" with regard to which the fish should show its diurnal activity pattern or its photopreferendum; a model to be schooled with; an obstacle to be avoided, etc. Now that we begin to understand something about the refined ways in which the visual information is coded and processed in the animal and used for releasing and steering its activities, serious doubts must be raised as to whether such simplified visual environments can deliver adequate information to all integration levels involved in the performance of the fish's natural behaviour. The inference seems to be inevitable that unnatural behaviour at a low level of integration must not only result from electrical stimulation of neural structures governing low levels of integration, or of damage to neural structures governming high levels of integration, but, besides, from an artificial stimulus situation simplified or distorted to such a degree that higher integrational levels do not receive the sensory information they are attuned to. This means that we run a serious risk of over-estimating the level of integration and thus of the biological consequences of a behaviour pattern when we say of a fish swimming in a tank with a moving ball that it schools with the ball; of a fish remaining close to some stationary object that it seeks shelter; of a fish remaining significantly longer in some part of a gradient or at some distance from a light source that it has a preference for the "intensity" measured there in some way by the experimentator.

7 THE VISUAL ENVIRONMENT OF FISH

Both physically and physiologically there seem to be sound reasons for trying to get detailed knowledge of the normal visual environment of fish.

Light fields under water have been studied intensively by physicists, both theoretically and experimentally. The flux distribution of light under water, and effects such as the deterioration of image contrast along the path of sight can be predicted from the interactions of light with the scattering-absorbing medium water. Moreover, new measuring instruments have been developed and the urge for standardization has been stressed. The results of work in various parts of the world have been extensively reviewed (Tyler, Preisendorfer, 1962; Duntley, 1962) and have recently been used for estimating vision in fish (Hemmings, 1966; Lythgoe, 1966).

The influx at a given point under water is displayed by the radiance distribution solid at this place. The shape of this solid is determined by assembling around the point in question the vectors whose lengths are proportional to the radiances measured in various directions by a rotating radiance tube (although its angular field of view influences the form of the radiance distribution solid, various workers have used tubes with arbitrary and various fields of view).

When trying to get some idea about the interest of the radiance distribution for an understanding of fish behaviour we must start with the assumption that a fish, selecting or diurnally changing its environmental preferendum either by movements in a horizontal or in a vertical direction, does so because the behaviour is first released by certain stimuli and then directed by others. In terms of phototaxis, the releasing of the behaviour is generally assumed to have something to do with a light "intensity" and the directing with a light "direction". On closer examination we have, however, no clear idea as to which parameters are used by the fish for determining the "intensity" and the "direction". For the time being a sound basis for further work seems to be the assumption that both must be derived from the angular radiance distribution: the "intensity" information which, we assume, releases the behaviour must be derived from some summating integration of the various vectors, whereas the directional information which presumably directs the behaviour must be derived from the situation of large or small vectors in the angular radiance distribution or, more generally, from the shape of the radiance distribution solid. Similarly, the angular radiance distribution probably directs the upward or downward escape reactions released in fish by an approaching or by an encountered net or by predators. Directional aspects of the stimulus situation produced by the net or the predators and factors such as the direction of gravitation may also be involved.

Because the visual information is sampled via the eyes it is to be expected that the characteristics of underwater illumination, as brought out by the shape of the radiance distribution solid, are reflected in some qualities of the fish's eyes and in factors that influence underwater visibility. Recently reviewed work indeed shows convincingly that the pigments of the fish's eye as a basis for the overall sensitivity and for the ability to perceive contrast (Lythgoe, 1966) and the factors that influence the conspicuousness of nets (guiding or enmeshing fish) and of the fish themselves (schooling) (Hemmings, 1966) cannot be understood without detailed data about the angular light distribution at the location under consideration.

From the complicated ways visual information is being sampled, analyzed and used for releasing and directing behaviour as pictured above, the most plausible inference seems to be that a more or less natural flux distribution is essential for behaviour to reflect its natural biological consequences. This means that out of the range of radiance distribution solids between the two theoretical extremities, namely a sphere (completely diffuse light) and a line (a parallel shaft), only a restricted group must be assumed to be useful for fish as a basis for natural behaviour. Light fields with radiance distribution solids either more towards a sphere or towards a line must be considered to be open to suspicion with respect to the interpretation given of the behaviour of fish in such light fields.

The problem of relating light measurements to behaviour has generally been underestimated. For convenience, the "intensity" is often derived from measurements with a horizontal plane surface and the "direction" from the location of the illuminating light source. It will be clear from the above data and considerations that this approach is an oversimplification of the problems.

Recently we have embarked on a research program with among other things the following aims:

1. measurements of angular radiance distributions under field conditions and under controlled illumination conditions

2. mathematical characterization of radiance distribution solids in the theoretical range between a sphere and a line; efforts will be made to incorporate not only physical parameters in this mathematical approach, but also physiological ones, namely the rules according to which visual information might be processed by the neural structures in the animal

3. estimation of the level of integration of behaviour observed in fish and other animals under divergent experimental visual stimulus conditions; inquiry into correlations between the range of radiance distribution solids permitting natural behaviour in a given animal, and the illumination conditions in its habitat.

8 PRELIMINARY EXPERIMENTS WITH FISH

Finally, in order to give some idea of the experimental approach, some initial experiments with fish will be described briefly. Full reports will be published elsewhere.

a. The three-spot gourami (Trichogaster trichopterus L.) seems to indicate with the elongated threadlike ventral fins whether or not visual information is received. In the dark or after extirpation of the eyes, these threadfins are put in a forward position and used as tactile organs. After extirpation of only one eye the ipsilateral threadfin is put forward (Weber, 1963). We have found that the threadfins are also put forward by intact animals under two extreme illumination conditions: first, when the radiance distribution solid is shifted in the direction of a sphere by an increased scattering of the light obtained by the introduction of a white $BaSO_4$ suspension into the aquarium water; and, secondly, when the radiance distribution solid is shifted in the direction of a line by illuminating a tank with flat black walls with a Zirconium oxide lamp (light source surface 0.13 mm^2; brightness 2000-5000 $cd\ cm^{-2}$) placed under water. Although under both illumination conditions the eyes as such are stimulated, the animal as a functional unit indicates that it does not receive adequate visual information. Unfortunately, most fish do not indicate by overt behaviour whether or not they receive adequate visual information.

b. Several species of fish, solitary as well as schooling ones, are being tested for their "light-preference" in a tank illuminated from one side. The orientation of the fish and their location in the light field produced are recorded by time-lapse cinematography. In one series of experiments the illumination conditions are changed in several ways, however, without changes in the spectral composition of the "white" light, and so that the irradiance measured by a flat surface, placed horizontally or vertically at a reference point in the tank (a measuring technique used in many expeiments described in the literature), is kept at a constant value. The preliminary results are that changes in the dimensions and the brightness of the light-source surface, and in the shade of the walls (matched to each other with respect to the irradiance requirements given above), effect the behaviour of the fish (for instance their mean orientation and location in the light field) in complicated ways, which, for the time being, are difficult to analyze. This means that such types of experiments are not likely to give easily interpretable and mutually comparable results with regard to items such as the fish's "preference" for certain "intensities". For "colours", things are still more complicated, because of the need for using physiologically equal irradiance intensities on the basis of the fish's visibility curve. During these experiments the dorsal light reaction was not observed when the tank was illuminated by a point-source of light. In some cyprinids, schooling proved to be disturbed or absent under such illumination conditions.

c. Fish (and other animals) are observed in a cylindric plastic container with either flat white or flat black walls and bottom illuminated from above through white opaline glass. The animal's movements are again recorded by time-lapse cinematography. In such a simplified visual environment the orientation and the location of some fish proves to be determined surprisingly rigidly, especially when simple visual stimuli are introduced into the container. Because of their relatively quiet way of swimming, we have started these experiments with some species of sunfish (Centrarchidae) and cichlids (Cichlidae), and with some ruff (Acerina cernua L.) and small pike (Esox lucius L.). The visual stimulus used was a ball 2.3 cm in diameter: a flat black one in a white container and a flat white one in a black container. In some experiments one eye or one lateral line nerve was extirpated. The preliminary results are that the fish have a strong tendency to keep contact with the wall, especially with the side without eye or lateral line nerve; that they keep the visual stimulus in their field of vision; and that they remain close to the visual stimulus. For these purposes the fish sometimes make very peculiar movements.

When these reactions occur with respect to a black ball in a white environment, one might think of the skototactic reaction frequently observed in insects under similar conditions. Jander (1965) has recently advocated the general opinion that the skototactic animal seeks "shelter", whereas the animal moving towards a light place (light source) would seek "free space". This might exemplify the overestimation of the level of integration and thus of the biological consequences of the animal's behaviour, because Michieli (1963) demonstrated convincingly that the skototactic reaction of several insects has artefactic aspects and that it is doubtful whether it is sensible always to look for its biological purpose (see also Campan, Medioni, 1963).

The fact that in our experiments the fish's movements with respect to the black balls in a white environment were similar to those with respect to a white ball in a black environment seems to confirm the danger of overestimating the biological consequences of the reactions of animals under artificial stimulus conditions. Whether we are here at the basis of the phenomenon that fish concentrate in the vicinity of objects placed in the water, so that they can be caught relatively easily remains to be seen.

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A COMPARISON OF ACOUSTIC THRESHOLD IN COD WITH RECORDINGS OF SHIP-NOISE

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Abstract

Acoustic threshold levels have been obtained for cod in conditioning experiments. Frequency response for pure tone signals are maintained in a frequency range of 50 to 540 Hz. The thresholds vary with frequency of stimulus and distance between fish and sound source, from -7dB to +25dB related to 1 μbar. Comparison of the threshold levels with the noise levels generated by two research vessels shows that ship noises would be perceived by cod at distances up to at least 70 to 80 m. The possibility of directional hearing in cod is also discussed and verified by experiment.

COMPARAISON ENTRE SEUIL D'AUDIBILITE DE LA MORUE ET ENREGISTREMENTS DU BRUIT DES NAVIRES

Résumé

Le seuil d'audibilité de la morue a été mesuré lors d'expériences de conditionnement. Dans le cas de sons purs, la réponse de fréquence se maintient pour la gamme allant de 50 à 540 Hz. Le seuil varie avec la fréquence du stimulus et la distance entre le poisson et la source du son, de - 7 dB à + 25 dB pour 1 microbar. En rapprochant les seuils d'audibilité d'enregistrements du bruit produit par deux navires de recherche, on a constaté que le bruit des navires serait perçu par la morue à des distances d'au moins 70 à 80 mètres. La communication traite également de la possibilité qu'existe chez la morue une audition directionnelle, vérifiée par l'expérience.

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DETERMINACION DEL UMBRAL ACUSTICO DEL BACALAO CON REGISTROS DE SONIDOS DE EMBARCACIONES

Extracto

Se han obtenido umbrales acústicos para bacalao en experimentos encaminados a crear reflejos condicionados. La frecuencia de réplica para señales de tono puro se mantiene en la gama de 50 a 540 Hz. Los mínimos perceptibles varían con la frecuencia de los estímulos y la distancia entre el pez y el origen del sonido, y van de -7dB a +25 dB relacionado a 1 micro Bar. La comparación del umbral de percepción y la intensidad del ruido generado por dos embarcaciones para investigaciones, demuestra que el bacalao lo percibe a distancia por lo menos hasta de 70 a 80 m. Se examina y se verifica mediante experimentos la posibilidad de que en el bacalao exista el oído direccional.

1 INTRODUCTION

The question of possible influence of noise generated by fishing gears and fishing vessels, on fish behaviour, was taken up for consideration in 1963 by the Norwegian Working Group for Development of Pelagic One-boat Trawl (A.P.E.). As a preliminary approach to this difficult and complex problem some basic studies on the audible capacities of fish were carried out, assuming that a comparison of the data obtained with the recordings of ship-noises might help elucidate the problem and indicate the prospects of continued studies in this field.

2 ACOUSTIC THRESHOLD IN COD, *Gadus morhua*

2.1 Test procedure

Cod was chosen for the experiment since this fish is easy to handle and train, and is one of the most common commercial species.

By applying a modified classical conditioning technique with feeding, average threshold values for sound stimuli perception were determined, with attention to the possible effect of change in distance between the fish and the sound source which varied from 0.5 to 4 m in the present experiments. The conditioning experiments were undertaken in a 6 x 3 x 1.5 m concrete tank, and to maintain control the fish were held in accage of nylon netting. The sound stimuli applied were pure tone signals, generated by an underwater loudspeaker. For signal control and calibration a small, calibrated pressure-sensitive hydrophone was used.

2.2 Results

The results are illustrated in Fig. 1. Stimulus response was maintained within a frequency range of 50 to 540 Hz. The sound thresholds at a given frequency, presented as sound pressure, changed from -7 to +25dB/ re 1 μbar

At the 4 m distance the threshold values decreased from 25dB at 540 Hz to about 13dB at 330 Hz. Further decrease of frequency did not appreciably affect the threshold level. No response was obtained at frequencies below 145 Hz. At the 0.5 m distance the threshold values decreased continuously with decreasing frequencies, down to -7dB at 50 Hz. The effect of distance from the sound source on the threshold frequency, particularly below about 400 Hz, is very graphically demonstrated by the two curves in Fig. 1.

2.3 Discussion

Comparing the observed capacities of sound perception in cod, with published data on other species, it would appear that the auditory capacities of cod are rather poor. In fact, cod have a minimum threshold of 49dB above the minimum threshold of the annular bream *Sargus annularis*, which has the highest sensitivity to sound stimuli so far reported (Dijkgraaf, 1949).

During the experiment higher sound intensities than anticipated were found necessary for stimulations, and the underwater loudspeaker used proved to be a bit weak. The observed frequency response could probably have been somewhat extended with a more powerful sound source.

By far the most surprising result, however, is the apparent change in sensitivity to sound stimuli with the change in distance between the fish and the sound source. It should be remembered that the observed threshold values refer to the minimum sound pressure for a stimulus response, measured where the fish is situated. If sound pressure is the only actual stimulus, obviously this value should remain constant and independent of the distance to the sound source. However, by approaching the source the fish seems to receive some additional stimulation which the pressure sensitive hydrophone does not pick up.

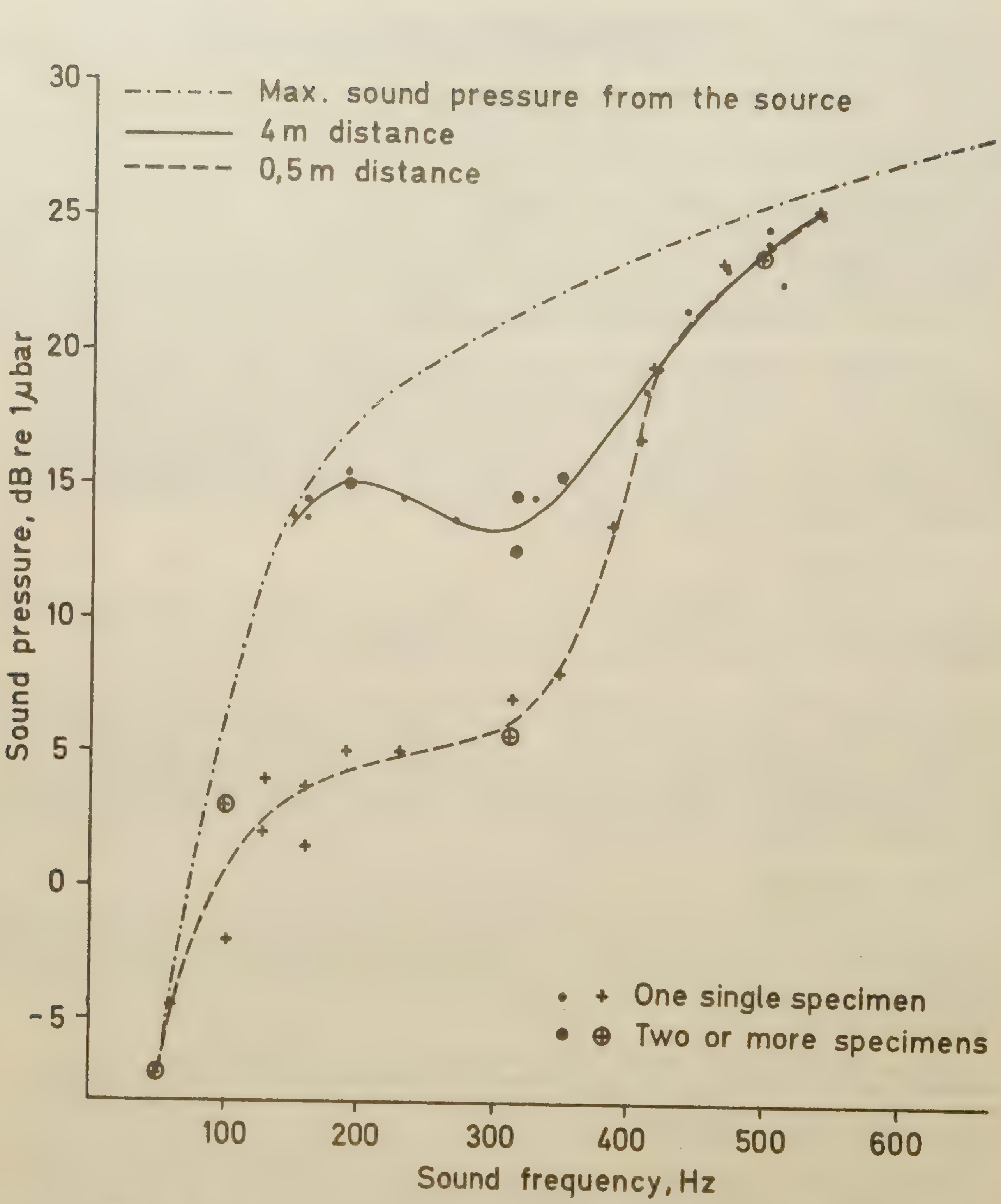

Fig. 1 Variation in sound pressure threshold with frequency and distance between fish and sound source.

Problems related to this matter are among the most debatable ones in conditioning experiments cited in literature (Harris and van Bergijk, 1962; Enger, 1966). It is beyond the scope of this paper to take up a full discussion of the problem, but some of the aspects should still be pointed out.

It is known that in an acoustic signal in water at least four different physical effects are present. These are, in addition to sound pressure, particle displacement, particle velocity and particle acceleration. If other physical effects than sound pressure are involved in a sensory stimulation, sensory organs other than the fish-ear must participate in the perception. These organs could be the lateral line organ or skin receptors (Harris and van Bergijk, 1962; Dijkgraaf, 1963).

In the present experiment there might have been a complex sound perception, with different sensory systems. An excellent argument in favour of this possibility is that the magnitude of particle displacement, particle velocity and particle acceleration at threshold values of sound pressure, within very small tolerances, can be shown to be independent of the distance to the sound source (here verifiable only for frequencies above 145 Hz. Perception by the lateral line organ or skin receptors could, therefore, be the explanation. For frequencies above 350 to 400 Hz where it seems correct to maintain the auditory thresholds as sound pressure thresholds, ear perception is more probable.

It should be emphasized that these experiments were undertaken under laboratory conditions, and it is open to question whether the results obtained here will hold for sound perception in cod under natural conditions.

Under far-field sound conditions, i.e. at distances above the wavelength/2π, a linear regression exists between the sound pressure and particle effects. This means that we may well express the auditory thresholds as sound pressure thresholds even if it is not biologically correct through the whole frequency range. Only under near-field conditions when the particle effects increase drastically as compared with sound pressure, will observed sound pressure thresholds below a certain frequency give a false impression of the auditory capacities in cod.

Thus, during fishing operations, at distances greater than about 50 m, the estimated threshold values given in Fig. 1 at 4 m sound source distance, should be applicable. For frequencies less than 145 Hz, at least down to 50 Hz, it may be possible, according to calculations from the 0.5 m observations, to extrapolate the values from the curve (flat).

3 INVESTIGATIONS OF SHIP NOISE

3.1 Recordings and analysis

Acoustically a ship in action is a moving noise source radiating noise in the sea almost uniformly in all directions. At short distances (less than 200 to 300 m), when refractions can be neglected, it is possible from noise observations at a known distance to calculate the sound field set up by the ship.

The intention of this paper is to compare the obtained knowledge of the auditory capacities in cod with informations about noise qualities and quantities which may occur in fishing areas during fishing operations. Although this should include gear noise as well, this study, for various practical reasons, had to be confined to the noise generated by fishing vessels.

Two representative fishing research vessels, the R/V G.O. SARS (600 t, 1200 hp) and the R/V JOHAN HJORT (700 t, 1300 hp) were carefully tested in order to determine the noise generated when in operation. To avoid disturbances the noise investigations were undertaken in a deep sheltered fjord. From the measuring station, an anchored ship, tape recordings of the underwater noise were made when the ship passed by. The observation point was a hydrophone hanging 50 m below the surface and 550 m above the bottom. Ranges between the operating ship and the observation point were determined through radar observations. Each ship made four runs at full speed (11 kn) and four at reduced speed (8 kn).

The noise recordings were later subjected to frequency analyses. Each recording was analysed in 1/3 octave bands from a lower centrefrequency of 31.4 Hz up to 4.8 kHz. The low frequency response was limited by local wave disturbances. The high frequency response was limited by the hydrophone itself. In addition to this broad band analysis, attempts were made to establish spectral lines, i.e. narrow frequency bands of high noise intensity. The bandwidth used here was 1 Hz. Corrections for the transmission loss at each run were based on a theoretical two-ways transmission, one which was direct and the other a surface reflected energy component.

3.2 Results

The results of the analyses are shown in Fig. 2 which presents the frequency distribution of the recorded noise and some of the heaviest spectral lines found. The plotted noise levels are average values at different speeds for each ship. As a common standard for presenting such data the noise levels are reduced to index value of spectrum level, i.e. 1 Hz bandwidth and a distance of 1 m.

At full speed both ships showed a continuous increase in noise with decreasing frequencies, down to about 100 Hz. In this frequency range the noise levels were also roughly of the same order for both ships. Below 100 Hz, sharp differences between the two ships became apparent. At reduced speed the picture was very much the same as for full speed at frequencies above 4 to 500 Hz. Below these frequencies a great deal of reduction in the intensity of the noise appeared, at least down to the lowest frequency bands. At 100 Hz the noise levels were 50 and 51 dB respectively. The heaviest spectral lines varied from 56dB to 74dB.

For our purpose it is of little interest to go into further details of the noise distributions. When applying an analysing technique as in the present investigations, the reliability of the obtained broad band noise levels is very much related to the presence of heavy spectral lines. In the noise recordings spectral lines mainly occur in a frequency range below 100 Hz. Thus, the noise levels obtained at frequencies above 100 Hz appear correct, while the noise levels at frequencies below 100 Hz should be carefully verified.

4 COMPARATIVE DISCUSSION

At a certain distance from a ship the generated noise will have decreased to a level which will be masked by the sea state noise. When a ship is approaching, the generated noise exceeds the level of the sea state noise, and if the observation point is sensitive enough, the noise should be detected. This is true even when a fish or a school of fish acts as the observation point. When components of the ship noise exceed the ambient noise, the degree of perception would be dependant on the capacities of the auditory system of the fish.

From Fig. 1 it is evident that the threshold response to sound stimuli for cod is approximately constant at 13dB in a frequency range from 350 Hz down to 150 Hz and probably down to 50 Hz. This threshold should be about 37 to 38dB below the maximum level of the broad band noise at 100 Hz shown in Fig. 2. The noise levels in Fig. 2 were in reference to 1 m distance and this means that an additional transmission loss of 37 to 38dB should be permitted before the possibility for perception of sound stimuli is lost. Such a transmission loss corresponds to a distance of 70 to 80 m from the ship.

The possible effect of heavy spectral lines in ship noise as biological stimulus is a rather difficult question to discuss. From audio investigations of humans for example, it is known that masking of pure tone signals by broad band noise does exist, and is dependant on the intensity of the stimulus, especially of the so-called critical band. A critical band of white noise is meant to be of equal acoustic power as a pure tone signal in the centrefrequency of the band.

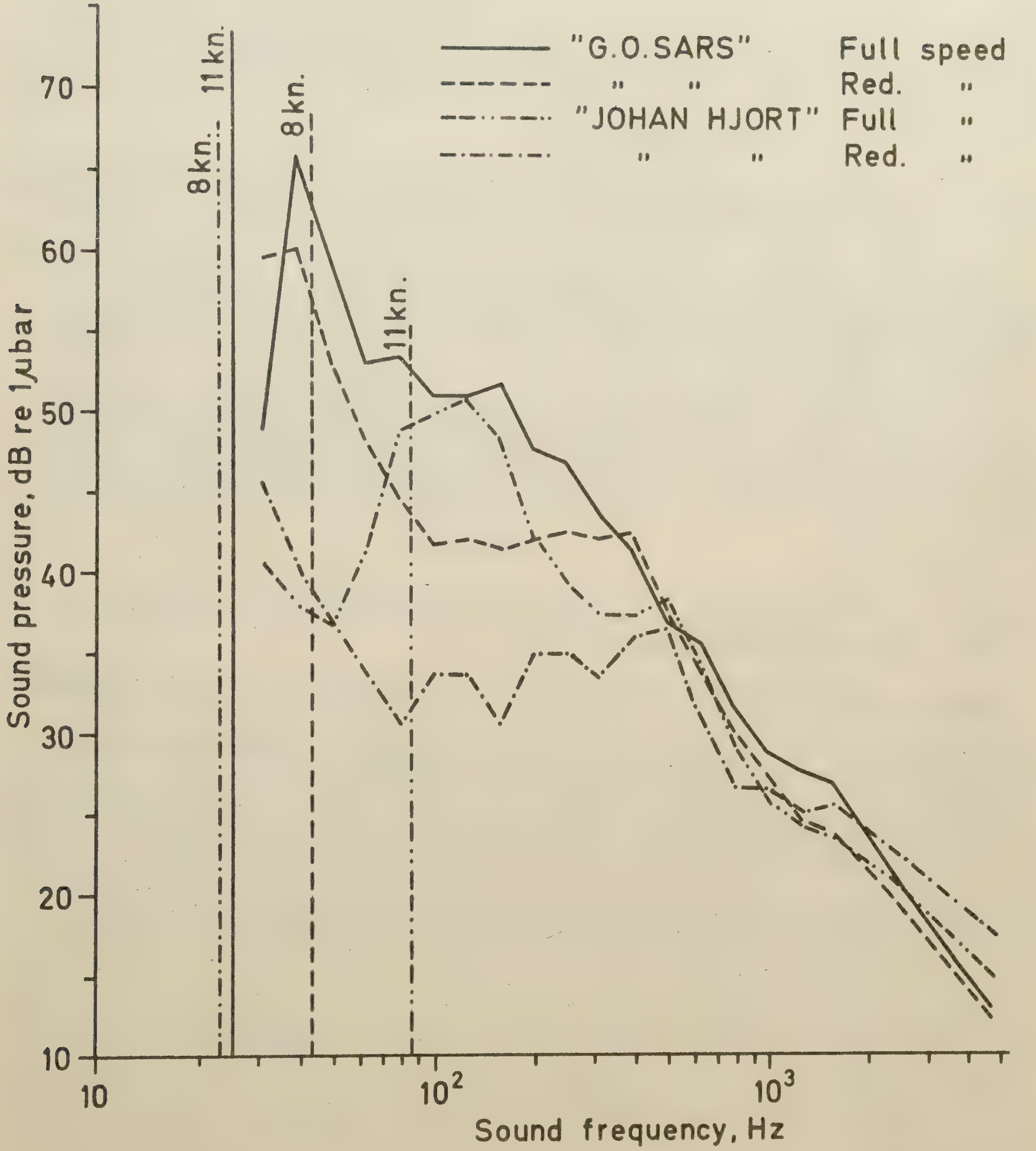

Fig. 2 Average frequency distribution of recorded noise (1/3 octave band) and heavy spectral lines (1 Hz band). (Index Value of Spectrum Level)

In our discussion this masking effect may indicate that when both broad band noise and spectral lines are present with the above stated threshold, a varying degree of masking may occur. Another aspect of this is the probability of broad band noise being more effective stimuli to fish than pure tone signals, when the levels of the stimuli are measured as sound pressure, and as here, equalised in bands of 1 Hz width. If these conclusions are true then the estimated range for biological stimuli of ship noise should be increased at least in case of sound pressure detection. However, according to the very insufficient knowledge of auditory capacities in fish such considerations should be treated most carefully.

An important question related to the problems which have been discussed in this paper, is whether fish possess the ability to determine the direction to a noise source or not. In practical fishing operations this should be one of the basic questions.

Although the importance of the particle effects in sensory stimuli is not completely understood, it is clear from the present experiments, that if the calculated thresholds of particle displacement, particle velocity or particle acceleration hold, it would indicate a far better possibility for directional hearing in fish than concluded from earlier investigations as well as from theoretical studies (van Bergijk, 1964).

In fact, it ought to be mentioned, that recent laboratory experiments have demonstrated the ability of directional hearing in cod for frequencies from 20 to 400 Hz. It has also been possible to show that this ability strongly depends on near field effects relative to the sound source. The level of this near-field effect, necessary for direction determinations, is in the order of magnitude of the earlier calculated threshold values.

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SWIMMING ACTIVITY OF THE SCOMBRID FISH EUTHYNNUS AFFINIS AS RELATED TO SEARCH FOR FOOD

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Abstract

The relation between swimming activity and food search was evaluated from the effects of time of day and food deprivation on typical swimming speeds and on responsiveness to food. Euthynnus affinis (35 to 42 cm fork length) were studied in outdoor tanks (7.3 m diameter, 1.1 m deep) that were illuminated at night (0.05 to 0.46 lux at the surface) so that the fish could avoid swimming into the walls. When sharing the tank with smaller live forage fish, E. affinis fed on these prey only during daylight. Likewise, their responsiveness to introduced food flavour at two deprivation levels, measured as increases in swimming speed, was greater during daylight (32 and 50 cm/sec) than at night (2 and 6 cm/sec). Responsiveness to food flavour also increased with duration of food deprivation. When food flavour was introduced to fish deprived of food for 2 to 5 h, swimming speed increased by 43 cm/sec whereas speed of fish deprived for 42 to 115 h increased by 119 cm/sec. In contrast, typical swimming speeds in the absence of food or food stimuli had no marked diel periodicity and did not increase with food deprivation. Recently captured fish swam continuously during daylight (80 cm/sec) and during the night (83 cn/sec). Speed declined by 20 percent in the first 24 h of food deprivation and 33 percent in the first 96 h of deprivation. Consequently, the amount of ocean searched by E. affinis would not be varied by changes in typical speed, but rather by changes in responsiveness to food. Typical swimming speeds must bring E. affinis in contact with sufficient food during daylight; but the speed is apparently regulated by biological requirements other than food search, perhaps hydrostatic equilibrium and gill ventilation.

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LA NAGE DU SCOMBRIDE *EUTHYNNUS AFFINIS* EN FONCTION DE LA RECHERCHE DE NOURRITURE

Résumé

L'auteur a étudié le rapport entre activité de nage et recherche de nourriture en se fondant sur l'influence de l'heure de la journée et de la privation de nourriture sur les vitesses caractéristiques de nage et sur la réponse à la présence de nourriture. Les travaux ont porté sur des *Euthynnus affinis* (mesurant de 35 à 42 cm à la fourche) placés dans des viviers (de 7,3 m de diamètre et de 1,1 m de profondeur) situés à l'extérieur et éclairés la nuit (de 0,05 à 0,46 lux à la surface) pour que les poissons puissent éviter de se heurter aux parois. Mis en présence de petits "poissons fourrage" vivants, *Euthynnus affinis* ne s'est alimenté de ces proies que durant la journée. De même, sa réponse à l'introduction d'une saveur d'aliment à deux niveaux de privation, mesurée en accroissement de la vitesse de nage, a été plus élevée le jour (32 et 50 cm/s) que la nuit (2 et 6 cm/s). La réaction à la présence de saveur d'aliment a également augmenté avec la durée de la privation de nourriture. Lorsqu'un goût d'aliment a été présenté au poisson ayant jeûné de 2 à 5 heures, la vitesse de nage s'est accrue de 43 cm/s tandis que l'accélération a atteint 119 cm/s pour le poisson privé de nourriture de 42 à 115 heures. Par contre, en l'absence de nourriture ou de stimuli alimentaires, les vitesses normales de nage n'ont pas révélé de nette périodicité nycthémérale et n'ont pas augmenté en cas de privation de nourriture. Des poissons capturés depuis peu nageaient sans interruption durant le jour (à 80 cm/s) et la nuit (à 83 cm/s). La vitesse a diminué de 20 pour 100 durant les premières 24 heures de jeûne, et de 33 pour 100 après 96 heures de jeûne. En conséquence, l'étendue du secteur océanique prospecté par *E. affinis* serait affectée par les modifications, non pas de la vitesse caractéristique, mais plutôt de la réponse à la nourriture. Durant la journée, *E. affinis* se déplaçant à sa vitesse normale doit venir en contact avec suffisamment de nourriture, mais la vitesse de nage est apparemment sous la dépendance d'exigences biologiques autres que la recherche de nourriture - peut-être l'équilibre hydrostatique et l'aération des branchies.

ACTIVIDAD NATATORIA DEL ESCOMBRIDO *EUTHYNNUS AFFINIS* CON RELACION A LA BUSQUEDA DE ALIMENTO

Extracto

La relación entre la actividad natatoria y la búsqueda de alimento se evaluó a partir de los efectos que ejercen el momento del día en velocidades típicas y sensibilidad al alimento. Se estudiaron ejemplares de *E. affinis* (de 35 a 42 cm de talla hasta la base de la aleta caudal) en estanques de 7,3 m de diámetro y 1,1 m de profundidad situados al aire libre e iluminados de noche (de 0,05 a 1,46 lux en la superficie) de manera que los peces no chocaran contra las paredes. Cuando en el estanque se ponían peces vivos forrajeros más pequeños, *E. affinis* solamente se alimentaba durante el día. Análogamente, su reacción a los alimentos saporíferos empleados en dos momentos de hambre, medida como un aumento en la velocidad de natación, era mayor durante las horas del día (32 y 50 cm/seg) que de noche (2 y 6 cm/seg). La reacción ante el alimento también era mayor cuanto más tiempo habían estado sin comer. Cuando los peces habían estado sin alimentos de dos a cinco horas, la introducción de sabor a alimento hacía que la velocidad natatoria aumentase a 43 cm/seg, en tanto que la de los peces que habían sin alimento de 42 a 115 horas aumentaban su velocidad a 119 cm/seg. Por otro lado, las velocidades de natación típicas cuando no había alimentos o estímulos alimentarios, no tenían una sensible periodicidad durante las 24 horas y no aumentaba con la falta de alimento. Peces recién capturados nadaban continuamente durante el día (80 cm/seg) y durante la noche (83 cm/seg). La velocidad disminuía en un 20 por ciento en las primeras 24 horas de estar en ayunas y en un 33 por ciento en las primeras 96 horas. Por tanto, las distancias recorridas en el océano en busca de alimento por *E. affinis* no variaría por razón de los cambios en la velocidad típica, sino por los cambios en la sensibilidad al alimento. Nadando a velocidades típicas, *E. affinis* debería encontrar suficiente alimento durante las horas del día, pero la velocidad parece estar regulada por necesidades biológicas distintas a la búsqueda de alimento, quizá por el equilibrio hidrostático y la ventilación de las branquias.

1 INTRODUCTION

The wavyback skipjack Euthynnus affinis (Cantor) (= E. yaito) feeds mostly upon smaller fishes and squids and large crustaceans (Tester and Nakamura, 1957; Kikawa et al, 1963; Kumaran, 1964). One would expect, as did Boddeke (1963), that some portion of the swimming activity of a scombrid might be determined by its need to search out its scattered and contagiously distributed prey in the relatively homogeneous environment of the upper mixed layer of the sea. But scombrids must also swim to maintain hydrostatic equilibrium and to ventilate their gills (Hall, 1930; Magnuson and Prescott, 1966; Magnuson, 1966). In this paper I evaluate the degree to which the swimming activity of E. affinis is related to food search. Inferences are drawn from the effects of time of day and food deprivation on responsiveness to food and on swimming activity.

2 EXPERIMENTAL CONDITIONS

E. affinis, of 35 to 42 cm fork length, were studied at a tank facility at Kewalo Basin, Honolulu (Magnuson, 1965). Water in the 7.3 m diameter tanks was 1.1 m deep. Temperature ranged between 22.8° and 25.9° C, and salinity between 32.8 and 34.6 °/oo. Temperature reached a midday peak of about 2° C higher than the night low, and during any 24 hours salinity was usually constant. Floodlights illuminated the tanks at night so that the fish could avoid the tank walls. In complete darkness the fish swam into the walls and were injured. In all but one experiment the tanks were exposed to the sun during the day. Surface illumination at night (from 0.05 to 0.46 lux) contrasted markedly with midday levels (ca 120,000 luxes).

Swimming activity was measured as swimming speed. The observer overlooked the tank from a window in an adjacent tower (Fig. 1). A Plexiglas[1] board overlaid with a thin sheet of clear plastic acetate was inserted horizontally into the frame of the window. The observer viewed the tank and the fish from a fixed position through the acetate and Plexiglas. The path of a swimming fish for a 30 second period was then traced on the acetate with a wax pencil. The length of the path was measured with a map measurer and converted to distance travelled and speed. The conversion factor depended on the distance between the observer's eye and the tracing board, and the tracing board and the tank. In the different tanks 1.0 cm on the board equalled 24 to 28 cm at mid-depth and 0.80 to 0.92 cm/sec swimming speed. The fish usually swam at mid-depth in the tanks, but speed would be overestimated by three percent for fish at the bottom and underestimated by three percent for those at the surface. Attempts were made to keep the eye position constant, and the timers and map measurers were routinely checked for accuracy.

Responsiveness to food was measured either as the frequency of feeding attacks upon live prey dwelling in the tank or as the increase in swimming speed that occurred when food flavour was introduced into a tank containing no food. The live prey were several thousand northern anchovies (Engraulis mordax) of about 9 cm fork length and Pacific thread herring (Opisthonema libertate) of about 11 cm fork length, and a few striped mullet (Mugil cephalus) of about 17 cm fork length. The invisible food flavour was made by immersing a thawed smelt (Osmeridae) about 10 cm fork length for 10 seconds in one litre of water taken from the supply to the tanks. The flavoured water was introduced from within the enclosed observation tower into the tank's water supply.

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[1] Trade names referred to in this publication do not imply endorsement of commercial products

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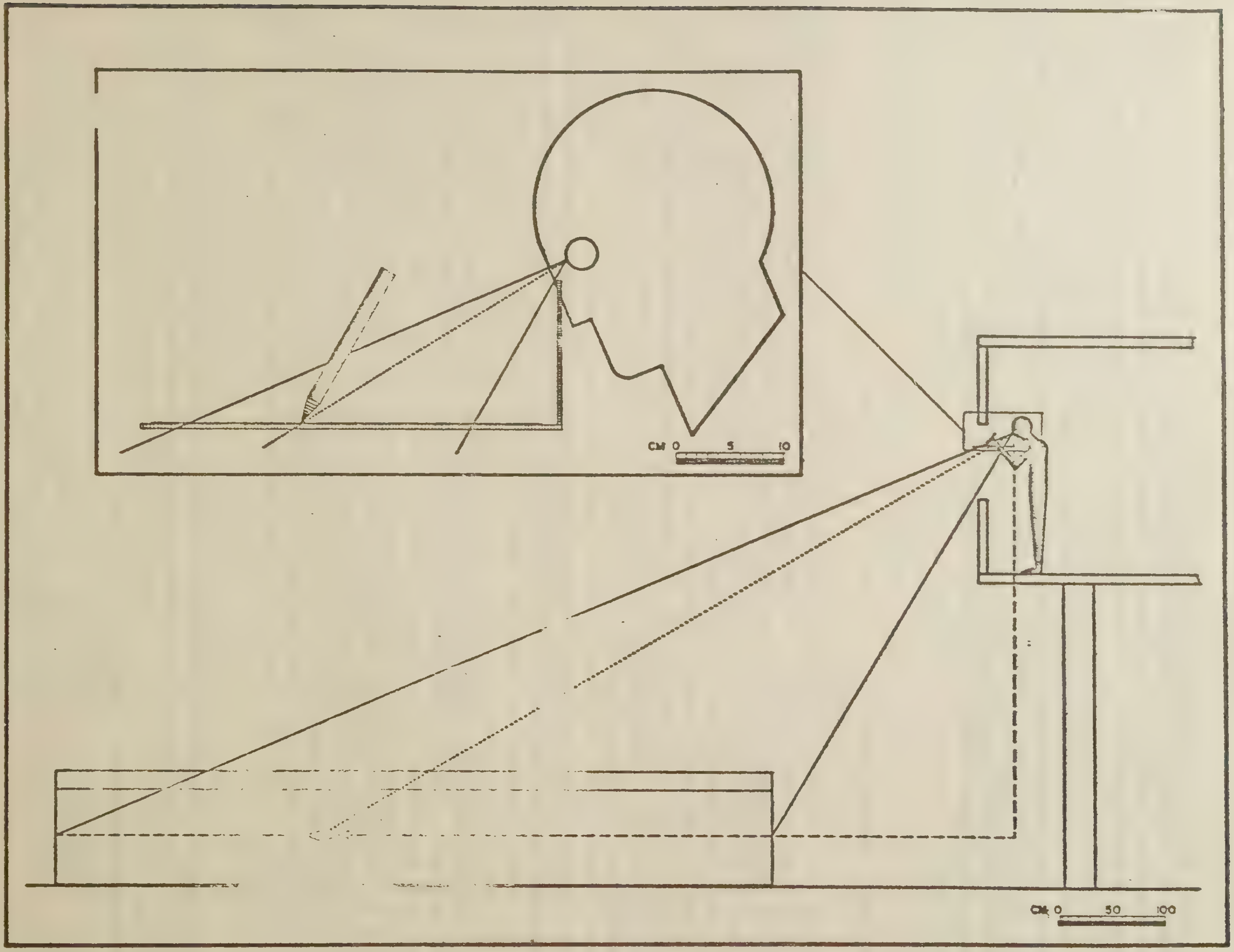
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Fig. 1 Diagram showing method of measuring swimming speed of E. affinis

The experiments were conducted intermittently from December 1963 to June 1966. Some inconsistencies in experimental design resulted from incorporating in our methods improvements that were developed during the 3-1/2 years and from utilizing for comparison data not originally collected for this study. The number of fish per tank varied because some died during experimentation and it was not always possible to procure equal numbers of live fish for each experiment.

3 CHANGES IN RESPONSIVENESS TO FOOD

The requirements of food search on swimming activity can be demonstrated from information on the changes in responsiveness of E. affinis to food. The influence of both time of day and food deprivation on the fish's responsiveness to food was examined.

3.1 Diel Rhythm

Diel changes in the amount of feeding activity were observed in a tank containing five specimens of E. affinis and several thousand live prey fish. The E. affinis of about 37 cm fork length had been in captivity for 1 to 1.5 months. The number of times that one or more of them made a feeding attack on individual prey was recorded for 45 minutes each hour during six 24-hour periods. These were averaged and expressed as number of attacks per 15 minutes.

E. affinis fed on the prey during daylight but not at night (Fig. 2). Feeding attacks were by far the most frequent from 0.5 to 1.5 hours after sunrise. Although not apparent in Fig. 2, on any one day, periods of intense feeding occurred at intervals averaging 2.5 hours, interspersed with periods of no feeding activity. Even in the confines of the tank E. affinis captured prey only with difficulty (the largest of the three prey species, M. cephalus, was never caught, and survived long after all the E. mordax and O. libertate had been eaten). Considerable time was thus spent in pursuit. During daylight the prey reacted to predation by forming compact schools and fleeing from the predators. At night E. affinis did not pursue the prey, nor did the prey react to the E. affinis swimming near them.

Responsiveness of E. affinis to a non-visual food stimulus, i.e., a food flavour, was measured both day and night. The species is known to respond to chemical extracts of food (Tester, 1959), by swimming faster, breaking the surface, ceasing to school, and returning to areas containing the extracts. Also they undergo a change in coloration (Nakamura and Magnuson, 1965). In this experiment the fish, of about 40 cm fork length, had been in captivity for 2 to 6 months. They were deprived of food for 6 and 30 hours. The experiment was replicated nine times with different fish. A tank contained one or two fish. Speed was recorded for four minutes before and four minutes after introduction of food flavour. The increase in speed was taken as the difference between the average speed before and after flavour was introduced. This was the only experiment during which a roof sheltered the tanks.

Responsiveness to food flavour was greater during daylight than at night at both deprivation levels (Table I). At night after six hours of deprivation, the swimming speed did not increase (Wilcoxon signed rank test, two-tailed, $n = 9$, $p > 0.25$). At night after 30 hours of deprivation, the speed did increase (Wilcoxon signed rank test, two-tailed, $n = 9$, $p = 0.02$), but the increase was only 12 percent of the increase during daylight.

Even during daylight the response to food flavour was brief. Within 15 minutes after its introduction the speeds were back to previous levels. Changes in direction of swimming were more frequent after flavour introduction.

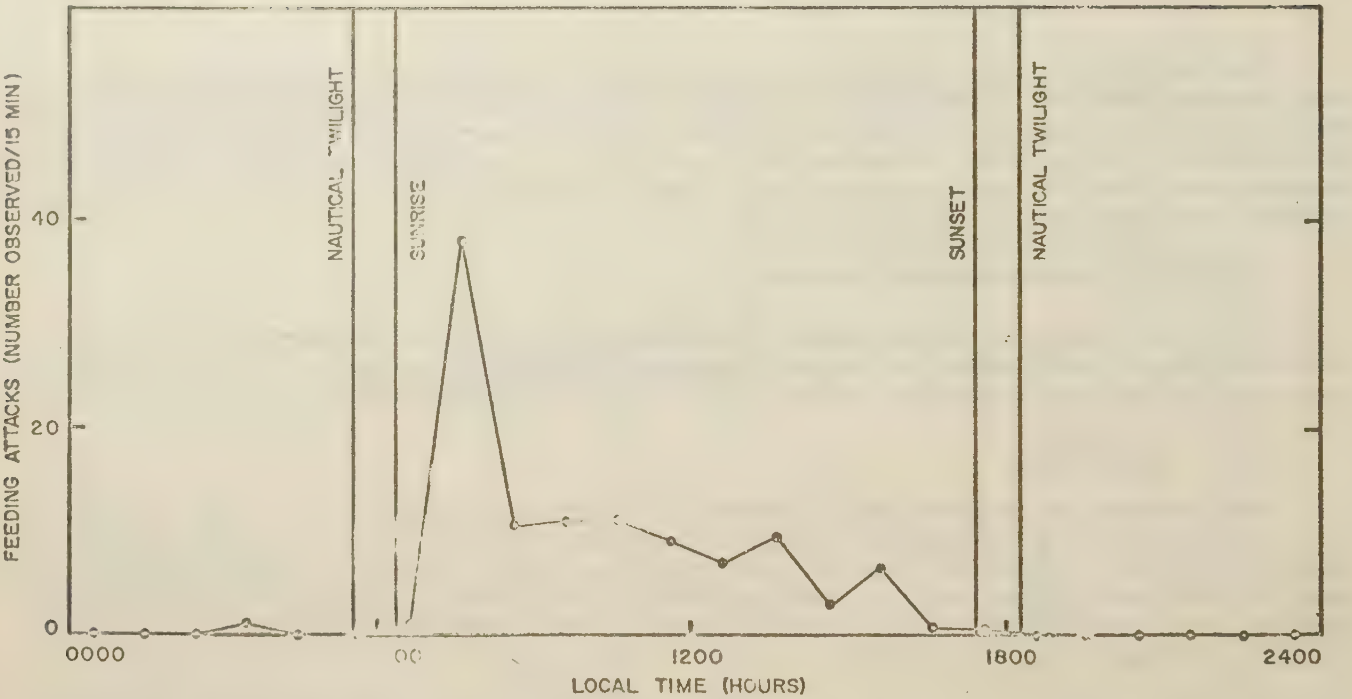

Fig. 2 Diel changes in feeding activity by E. affinis in the presence of several thousand live prey fish

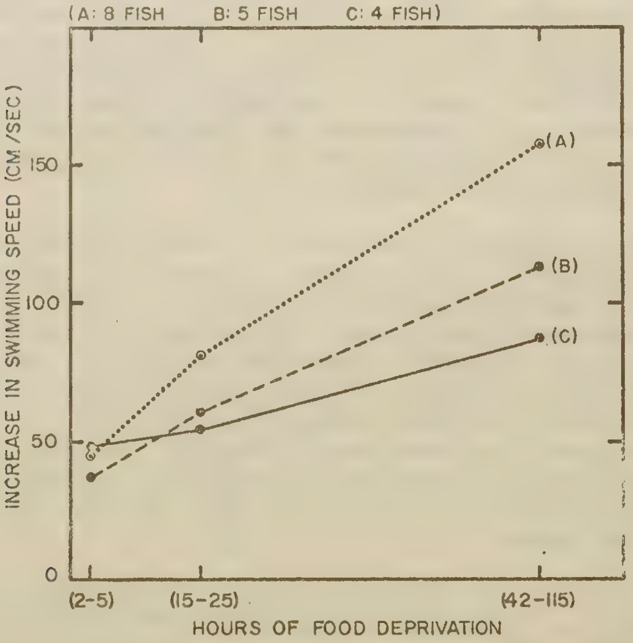

Fig. 3 The effect of food deprivation on the change in the swimming speed of E. affinis that occurred when food flavour was introduced. Each line represents a different tank.

TABLE I

Day and night comparison of the responsiveness of E. affinis to food flavour as measured by the changes in swimming speed that occurred when food flavour was introduced after the fish had been deprived of food for 6 or 30 hours

Hours of deprivation	Responsiveness to food flavour (change in speed/cm/sec)			
	Day		Night	
	Mean	Range	Mean	Range
6	+32	-8 to +95	+2	-6 to +14
30	+50	-4 to +108	+6	-1 to +23

The marked difference between responsiveness of E. affinis to food during the day and the night occurred even though the tanks were illuminated at an intensity that allowed schooling orientation to persist and permitted the fish to avoid swimming into the walls. The diel rhythm may be endogenous, but even if it is exogenous, E. affinis in the open sea would be expected to feed primarily during daylight because it is even darker at night in the sea than in the tanks.

3.2 Food Deprivation

Data on the effect of food deprivation on the response to food flavour were obtained from specimens of E. affinis of about 35 cm fork length that had been in captivity for one to two months. In each of the three tanks containing four, five, and eight fish respectively, five introductions of flavour were made after two to five hours of food deprivation, four after 15 to 25 hours of deprivation, and two after 42 to 115 hours of deprivation. The change in swimming speed resulting from flavour introduction was determined from one minute of speed measurement, five minutes before and five minutes after introduction of the flavour.

The responsiveness to food flavour was greater when the fish were deprived of food longer (Fig. 3). The average increases in speed after two to five, 15 to 25, and 42 to 115 hours of food deprivation were 43, 66, and 119 cm/sec, respectively. The increase was not the same for each deprivation level (Friedman two-way analysis of variance, $N = 3$, $k = 3$, $p = 0.025$). Greater responsiveness to flavour after longer deprivation periods was also indicated in the data presented in Table I.

4 CHANGES IN SWIMMING ACTIVITY

If food search plays the most important role in determining swimming activity of E. affinis, then swimming speeds during daylight, which is the period of feeding, should be noticeably higher than those during night. Similarly fish deprived of food longer should swim faster than recently fed fish. (See section 5.) The following experiments concern these two hypotheses.

4.1 Diel Rhythm

Diel changes in swimming activity of E. affinis were studied by measuring swimming speed every two hours from 0100 to 2300 hours in tanks containing no food. Measurements were made on fish of about 35 cm fork length that had been in captivity less than one month. They were not offered food on an observation day but had been fed thawed shrimp on the previous day at 0900 and 1600 hours. The experiment was repeated twice in each of the three tanks, which contained 7, 8, and 15 fish. Speed was measured each time for one minute, every two hours, in each tank.

Swimming activity persisted throughout the 24 hours in the absence of food and was no greater during the day than during the night (Fig. 4). The average speed of fish in any one tank was never less than 58 cm/sec. No fish swam slower than 48 cm/sec for any one minute interval. No fish ever stopped swimming. Average day speed was 80 cm/sec and the average night speed was 83 cm/sec.

Diel changes in speed of fish in tanks with no food were measured again after the fish had been in captivity 5 to 6 and 8 months. The fish were fed thawed smelt or beef liver on the previous day. These data totalled 276 minutes of speed measurements. Speed was lower than that of fish in captivity less than one month, but no marked difference was observed between the average day speed (74 cm/sec) and the average night speed (72 cm/sec). Only the fish held in one of the tanks for 5 to 6 months swam markedly faster during daylight. These data were included in the above averages.

Diel changes in swimming activity of E. affinis in a tank containing several thousand live prey fish were also studied by measuring swimming speed every two hours from 0100 to 2300 hours. Measurements were made concurrently with those feeding on prey fish. Swimming speed was recorded for four minutes every two hours for the six 24-hour periods.

In Fig. 5 the average speed of fish in tanks without food (from Fig. 4) is compared with the average for fish in tanks with live prey. The latter appeared to swim faster than those without food, even at night. The difference was less at night and may have resulted from the slight size difference between the fish in the two experiments and the difference between their levels of food deprivation, as explained in the next section. Those dwelling with live prey did swim faster during daylight than at night. Day speed averaged 108 cm/sec and night speed averaged 92 cm/sec. The higher average during daylight resulted from intermittent high-speed pursuit of the prey.

4.2 Food Deprivation

The effect of food deprivation on the swimming activity of E. affinis was studied by measuring swimming speed every 24 hours during three or five days of food deprivation. First measurements were made 0.5 to 2.5 hours after the fish had been fed thawed beef liver and smelt. The fish, of about 41 cm fork length, had been in captivity 6 to 7 months. Each of the three tanks held two or three fish. The experiment was repeated in each tank six times during midday, three times just before dark, and five times just after dark.

Swimming speed was highest after a meal and decreased when the fish were deprived of food (Fig. 6). The decrease occurred both during daylight and at night. The greatest change, a decrease of 20 percent, was in the first 24 hours. Speed asymptotically approached a low of about 55 cm/sec after the fish had been without food for four days. Other individuals of this species have survived in the tanks as long as 21 days without feeding. They continued to swim throughout the period.

5 BIOLOGICAL IMPLICATIONS

If the level of swimming activity of E. affinis is regulated for food search, swimming speeds should be higher during daylight when the fish can take advantage of a contact with prey. Availability of food has been considered important in determining the time that vertebrates are active (Cloudsley-Thompson, 1961), and diel cycles of locomotory activity are often associated with feeding in fish (Woodhead, 1966). Fish often display marked diel changes in activity (Carlander and Cleary, 1949; Kruuk, 1963; Darnell and Meierotto, 1965; Hergenrader and Hasler, 1966; Bohun and Winn, 1966). Some species are quiescent during the night (Hasler and Villemonte, 1953; Radakov and Solovev, 1959; Zaitsev and Radakov, 1960). A time-coordinated increase in activity occurs in certain fishes before feeding time and can be moved by changing the time that the fish are fed (Davis and Bardach, 1965). Locomotory activity of the common sole (Solea vulgaris) (Kruuk, 1963) and the longspine squirrelfish (Holocentrus rufus) (Winn, Marshall and Hazlett, 1964) is greatest at night when most feeding occurs. A more extensive review of diel changes of swimming activity as related to feeding in fishes can be found in Woodhead (1966).

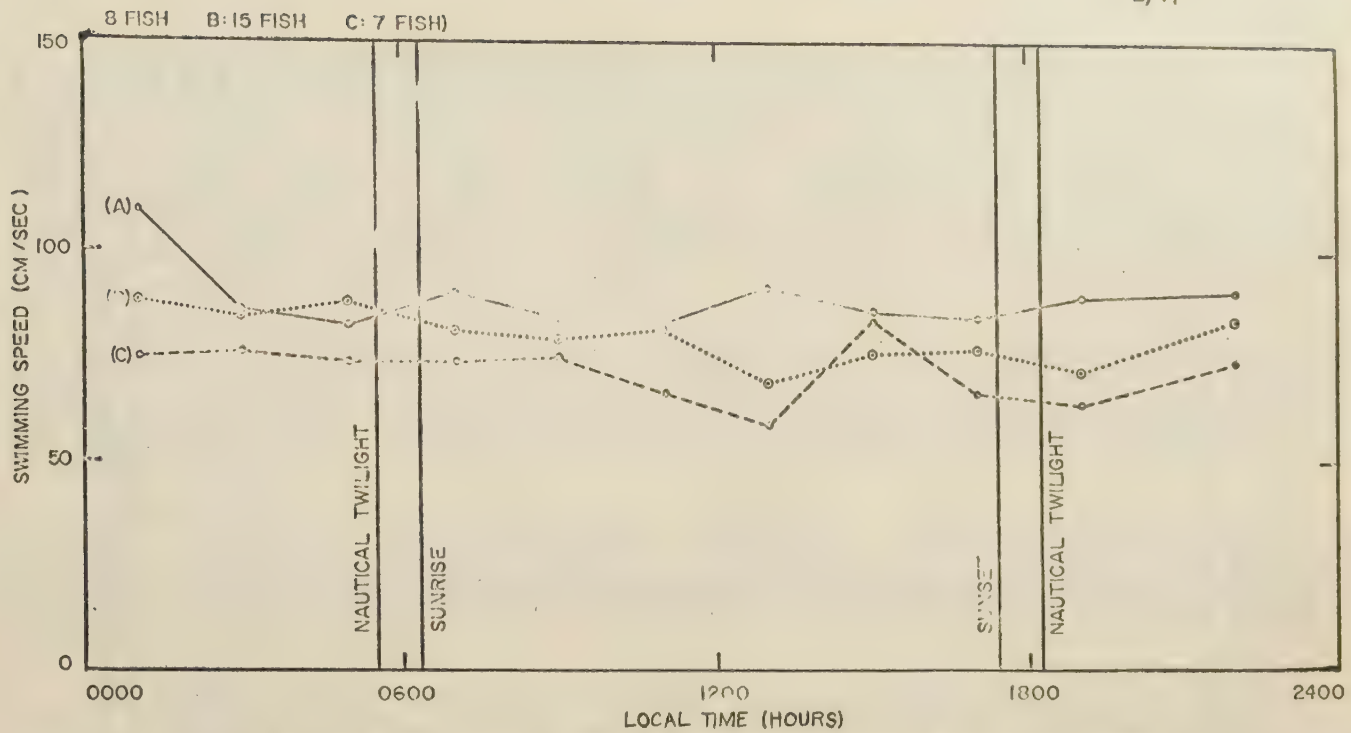

Fig. 4 Swimming speed of E. affinis in the absence of food and food stimuli throughout a 24-hour period. Each line represents a different tank. (Tanks A, B, and C cannot be equated to tanks A, B, and C in Fig. 3.)

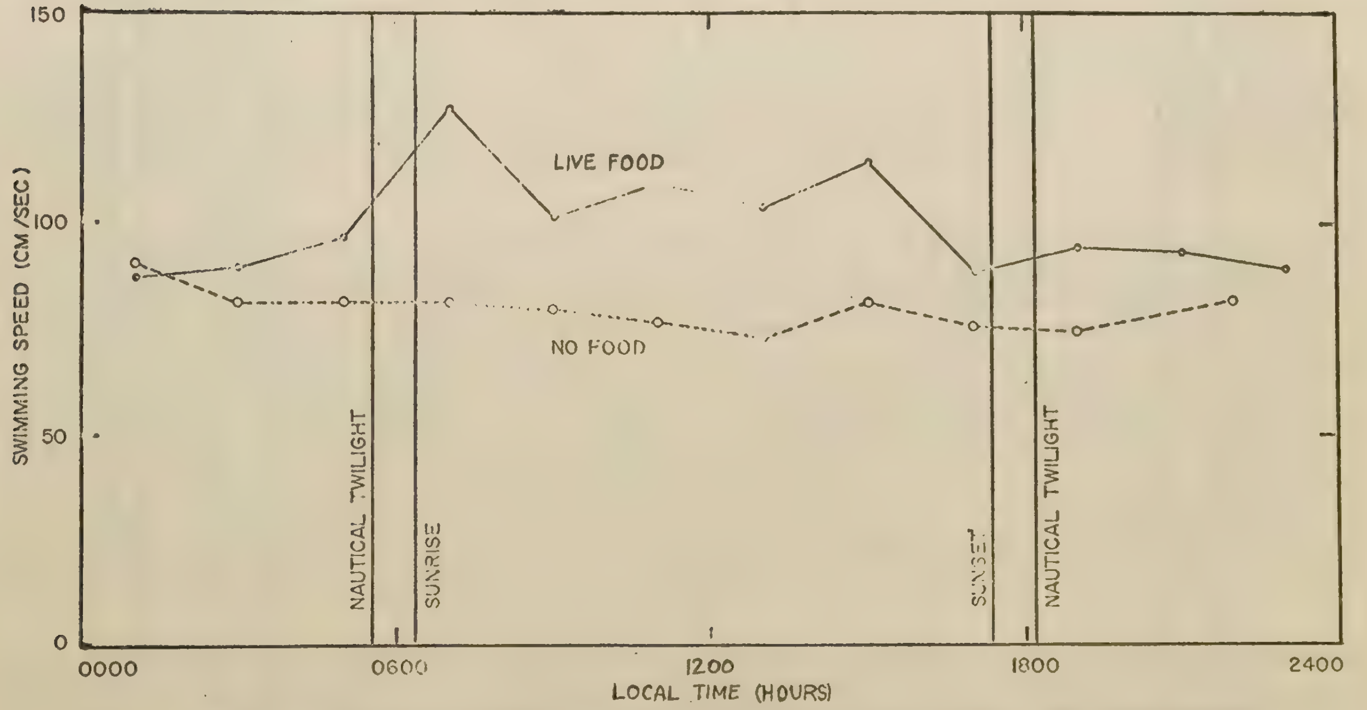

Fig. 5 Comparison throughout a 24-hour period of swimming speeds of E. affinis in a tank with live prey fish and in tanks containing no food or food stimuli.

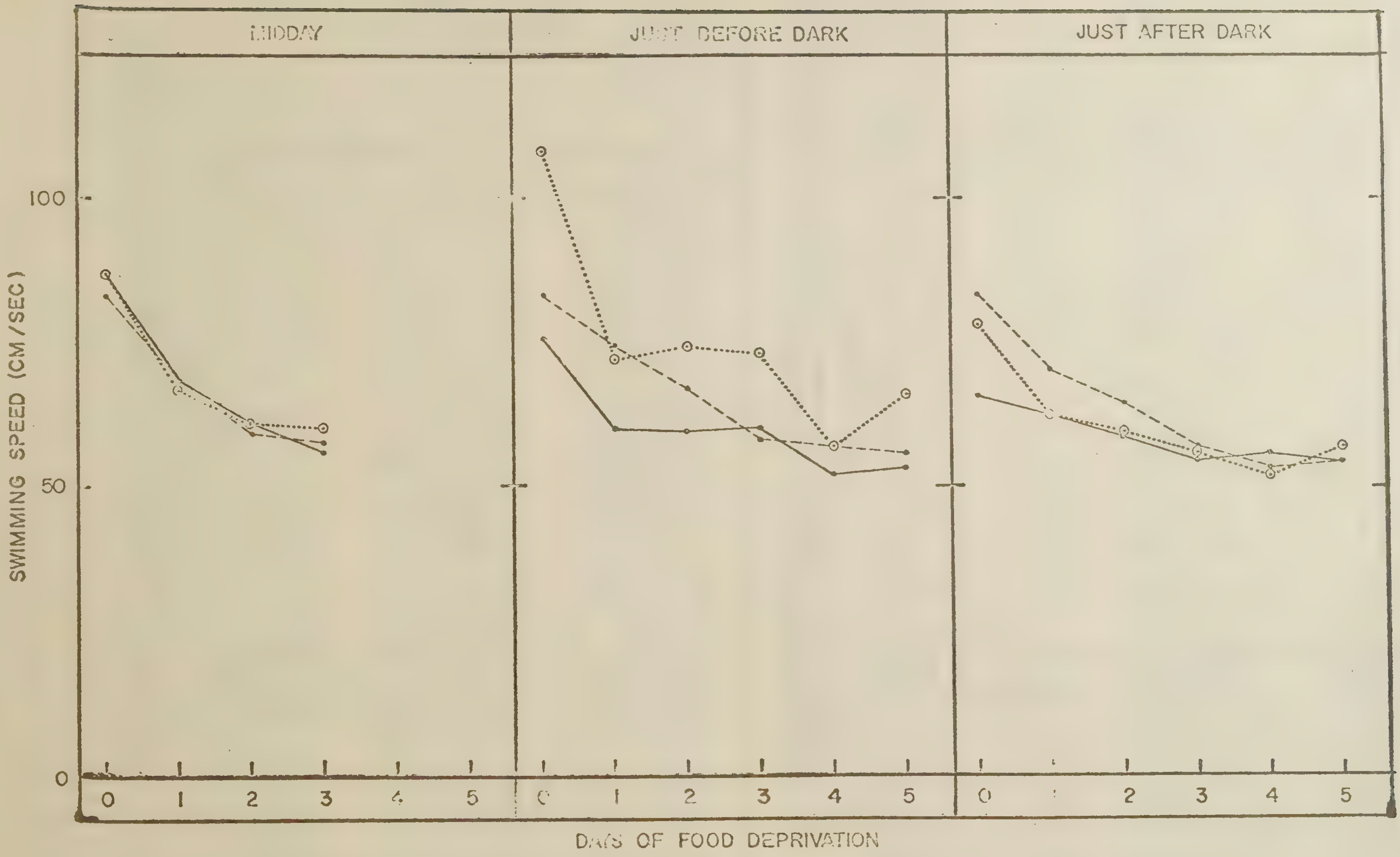

Fig. 6 Effect of food deprivation on the swimming speed of E. affinis at midday, just before dark, and just after dark. Each line represents a different tank.

In contrast to the diel changes in responsiveness to food, swimming activity of E. affinis has no marked diel periodicity. Recently captured fish (35 cm fork length) swimming at their average speed would have searched a 35 km path in 12 hours of daylight when no food stimuli were present. They also would have travelled another 35 km during a 12-hour night, and to no avail as far as food search was concerned. Even in the presence of live food, speed during daylight averaged only 1.17 times the speed at night. This slight increase resulted from intermittent periods of high activity during the day while the fish pursued live prey. Search was not a factor, because the fish were in continuous contact with the prey.

If the level of swimming activity is regulated for food search, swimming speed should be higher when motivation to feed is increased by food deprivation. A marked increase in locomotory activity that occurs among certain non-hibernating mammals during the first days of food deprivation may be associated with food search (Cornish and Mrosovsky, 1965).

In contrast to the increase in responsiveness to food during deprivation, the swimming activity of E. affinis decreased. It decreased by 20 percent in the first 24 hours and continued to decrease until four days of deprivation had passed. Swimming speeds after four and five days of deprivation were about 33 percent less than speeds of recently fed E. affinis.

The persistence of typical speed throughout the 24 hours, and the decrease in typical speed with food deprivation, are not consistent with the requirements of a behaviour regulated for food search. Speed during daylight must be adequate for locating sufficient food, but it must be regulated in response to some biological need other than search for food.

In contrast to the typical speeds, the temporary increase in speed that occurs when the fish are stimulated with food flavours does appear to heighten the intensity of food search at appropriate times for such activity. The increase in speed was much greater during daylight than at night. It was also greater if the fish were deprived of food longer. The increase more than compensated for the decrease in typical speed with deprivation.

Observed variations in swimming activity appear to be more closely associated with the requirements for maintaining hydrostatic equilibrium and gill ventilation than for food search. The fish is heavier than sea water and must continuously generate lift to overcome this weight (Magnuson, 1966). Because this weight is greater just after the fish eats, higher speeds would be required to generate the required lift just after a meal than after a period of deprivation. Gill ventilation is also a continuous requirement and in E. affinis is accomplished by swimming forward with the mouth agape. When the Atlantic mackerel (Scomber scomber) was prevented from swimming forward, the oxygen saturation of its blood decreased from 85 percent to 11 percent (Hall, 1930). The amount of gill ventilation required should also decrease with food deprivation. For example, the oxygen consumption of the aholehole (Kuhlia sandvicensis) decreased during periods of food deprivation even when swimming activity was held constant (Muir, Nelson and Bridges, 1965).

The demands of hydrostatic equilibrium and gill ventilation on swimming activity are continuous and apparently mask any periodic demands of food search on swimming activity. If we assume that these results apply to fish at sea, then the amount of ocean searched is not varied throughout a 24-hour period by changes in typical speed, but by changes in the responsiveness of food; during daylight food search is increased by higher swimming speeds only if food stimuli are detected.

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SOME OBSERVATIONS ON FISH SCHOOLS AND THEIR ENVIRONMENT

by

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Abstract

Fishes are believed to form schools in the presence of shelters, when attracted by food, or, during the breeding season.

This paper describes some observations made on the factors inducing the formation of fish schools in coastal fishing grounds. It has been found that topographical conditions and the position of water masses are related to the formation of schools and the direction and force of tidal currents influence their position.

QUELQUES OBSERVATIONS SUR LES BANCS DE POISSONS ET LEUR MILIEU

Résumé

On pense que les poissons se rassemblent en bancs en présence d'abris, lorqu'ils sont attirés par la nourriture, ou durant la fraie.

La communication rapporte certaines observations sur les facteurs déterminant la constitution de bancs sur les fonds de pêche des eaux côtières. Il a été constaté que les caractéristiques topographiques et l'emplacement des masses d'eau interviennent dans la formation des bancs, dont la position est aussi influencée par la direction et par la force des courants de marée.

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OBSERVACIONES SOBRE LOS CARDUMENES DE PECES Y SU AMBIENTE

Extracto

Se cree que los peces forman cardúmenes cuando están en presencia de refugios, atraídos por el alimento y durante la temporada de la reproducción.

Describe este documento observaciones realizadas sobre los factores que hacen que los peces formen cardúmenes en los bancos de pesca costeros. Se ha determinado que las condiciones topográficas y la posición de las masas de agua guardan relación con la formación de cardúmenes y la dirección y fuerza de las corrientes de las mareas influyen en su posición.

1 INTRODUCTION

It is of considerable interest and importance to fishermen to know when and where fishes concentrate. In recent years many artificial fishing grounds have been constructed in Japan. In the selection of sites for artificial grounds, a sound knowledge of the process of formations of fish schools is of utmost importance.

2 FACTORS INDUCING FORMATION OF FISH SCHOOLS

2.1 Fish schools in the open sea

During research voyages on the east coast of the Goto Islands, two kinds of charts were obtained, as shown in Fig. 1 and 2. Figure 1 is the record of a sonic fish-finder, and Fig. 2 the thermograph record of surface water temperature. The marks A to I on the charts denote the same positions on the voyage.

Two characteristics about fish school behaviour are apparent in these records. In Fig. 2 pelagic fish schools are found at marks A, C, D, F and H, and these coincide with fluctuations in water temperature. Bottom fish schools are recorded in Fig. 1 at marks B, C_2, E, G and I, with no apparent relation to water temperature. But the thermograph used indicated only the surface water temperature and so these records were inconclusive.

However, it appears that fluctuations in water temperature or geographical changes act as important factors that induce formation of fish schools.

2.2 Fish schools around reefs

In coastal fishing grounds fish schools are located near ridges and faults. Figures 3, 4 and 5 were obtained during the research voyage on the Nomo peninsula, near the Nagasaki, on 19 and 20 June, 1958. Figure 3 shows the course of this voyage; Fig. 4 is the record of the fish-finder during the onward voyage in ebb tide from north to south and Fig. 5 of the return voyage in flood tide, from south to north. In both cases, the fish schools are found in the lower section of the current some distance from the ridges.

Figure 6 shows the location of fish schools around flat reefs. This photograph was taken at about 5 mi east off the Narao port. In the neighbourhood of this area are good fishing grounds for hook and long line fishing of sea-bream. The sea bottom is flat and about 70 m in depth. We know that on rocky bottom the fish-finder records the long echo mark of the bottom line. In Fig. 6 some flat rocks are noticed in level with the surrounding area. It would seem that the turbulent currents do not occur under such topographical conditions. However, some fish schools were located at the edge of the reef.

2.3 Fish schools in channels

There are many channels and straits in Nagasaki and it is often possible to observe the behaviour of fish in the strait. In slack water, the fishes swim about and scatter themselves in the channel and it is not possible to find fish schools by echo fish-finders around the reef. When the tide turns, the tidal current moves slowly, the fishes come together around the reefs in the middle of the channel and form schools. The current draws close to half tide, and the velocity becomes strong, the fish schools around the reefs vanish and the fish form small groups against current in both side-inlets of the channel.

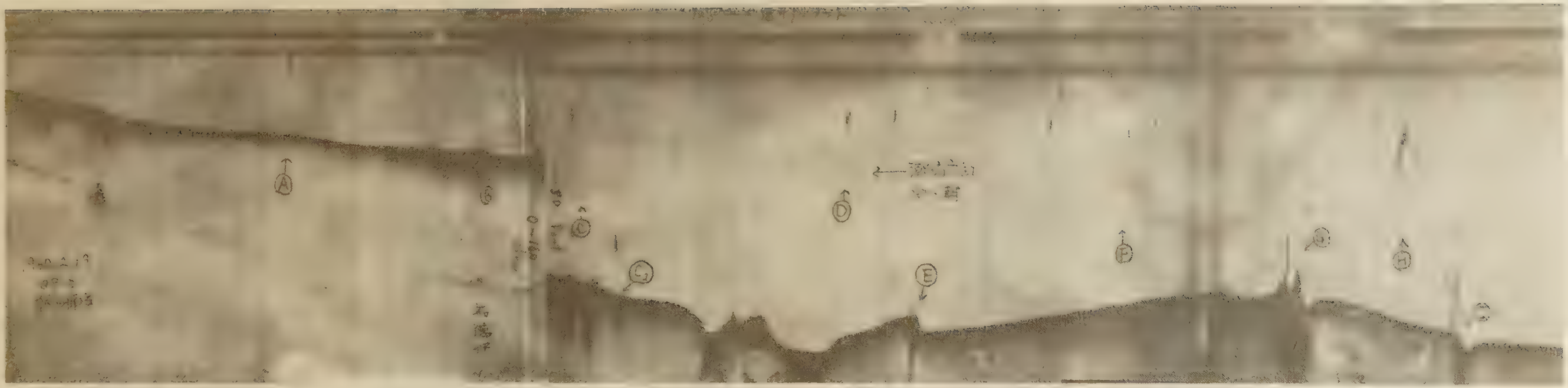

Fig. 1 The echogram of the fish-finder, obtained during the survey of the east coast of the Goto Islands, 19 February 1960.

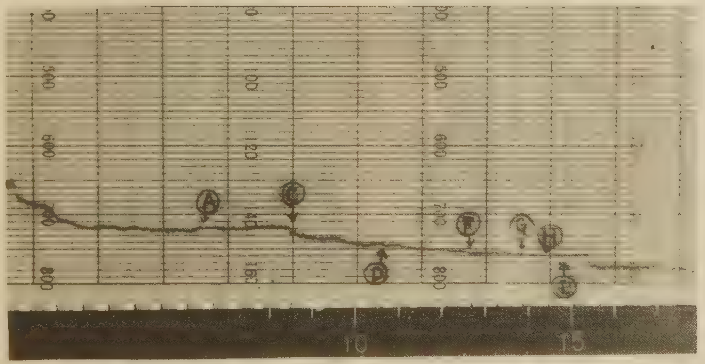

Fig. 2 The thermograph chart (off the grounds delineated in Fig. 1.)

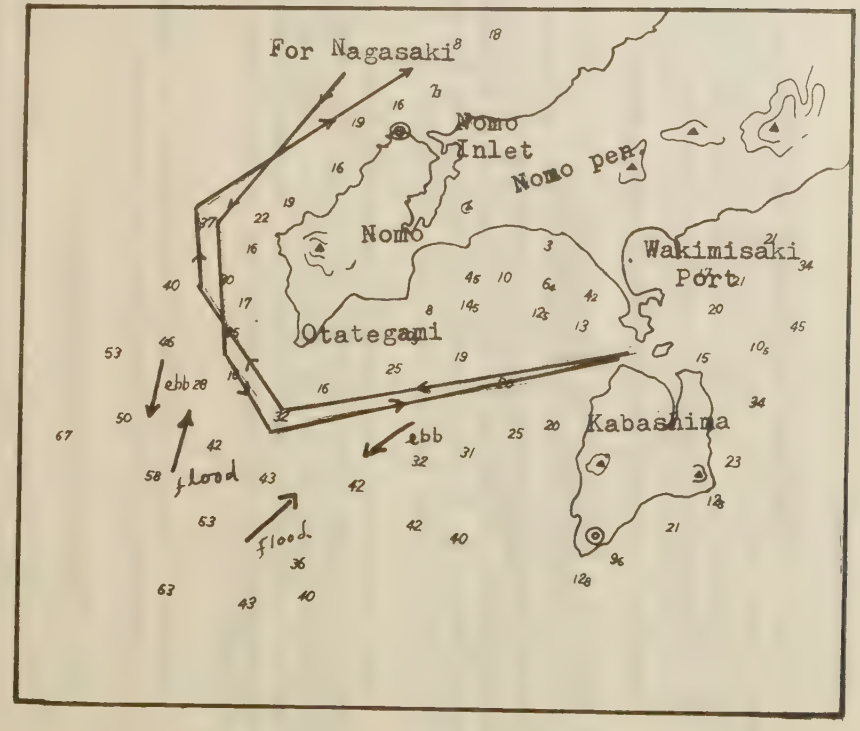
For Nagasaki
Nomo Inlet
Nomo pen.
Nomo
Otategami
Wakimisaki Port
Kabashima
ebb
flood
ebb
flood

Fig. 3 Navigation course of the research boat off Nomo peninsula.

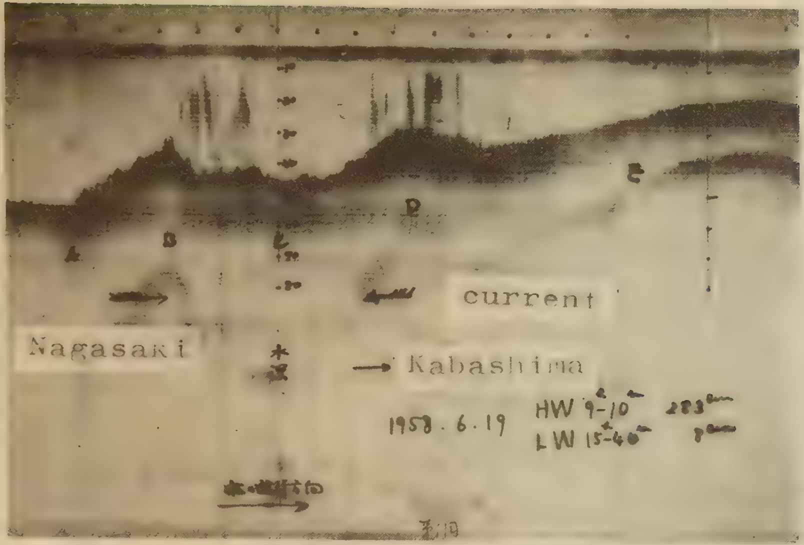

Fig. 4 The echogram of the fish-finder at Nomo, during the onward voyage, 19 June 1958; 1100 h at ebb tide.

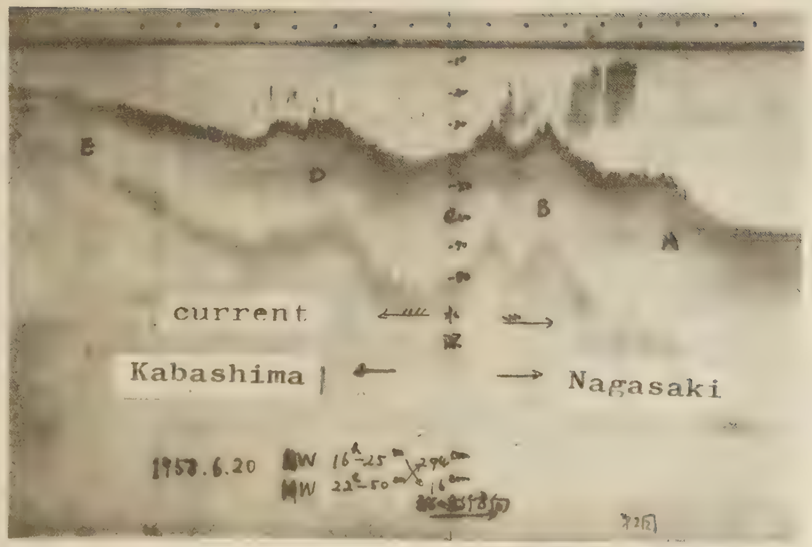

Fig. 5 The echogram of the fish-finder at Nomo, on the return voyage, 20 June 1958; 1630 h at flood tide.

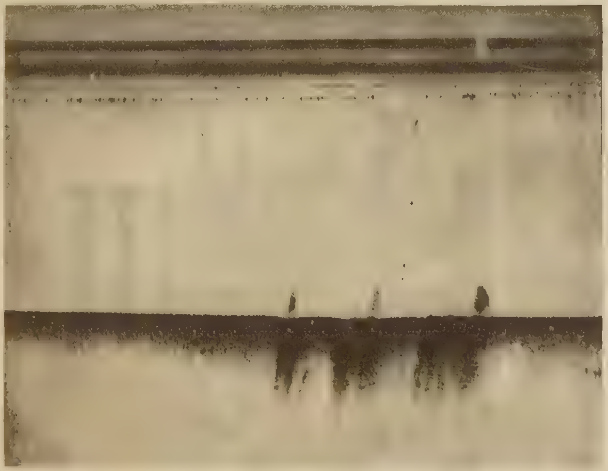

Fig. 6 The fish school above flat reefs at Narao.

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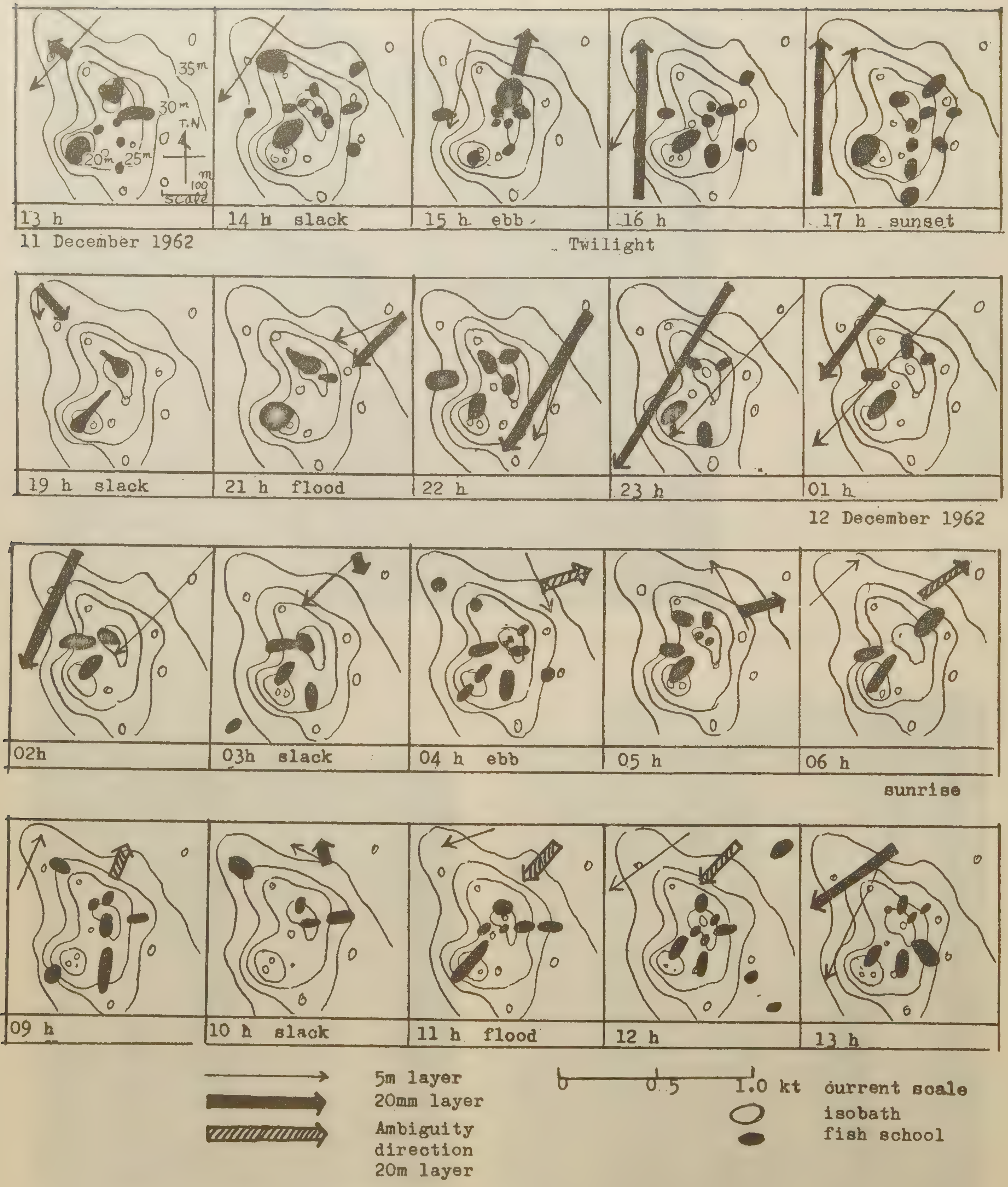
35m
30m
25m
20m
T.N
m
100
0
scale
13 h
14 h slack
15 h ebb
16 h
17 h sunset
11 December 1962
Twilight
19 h slack
21 h flood
22 h
23 h
01 h
12 December 1962
02h
03h slack
04 h ebb
05 h
06 h
sunrise
09 h
10 h slack
11 h flood
12 h
13 h
5m layer
20mm layer
Ambiguity direction 20m layer
0 0.5 1.0 kt current scale
isobath
fish school

Fig. 7 Diurnal variation of fish schools

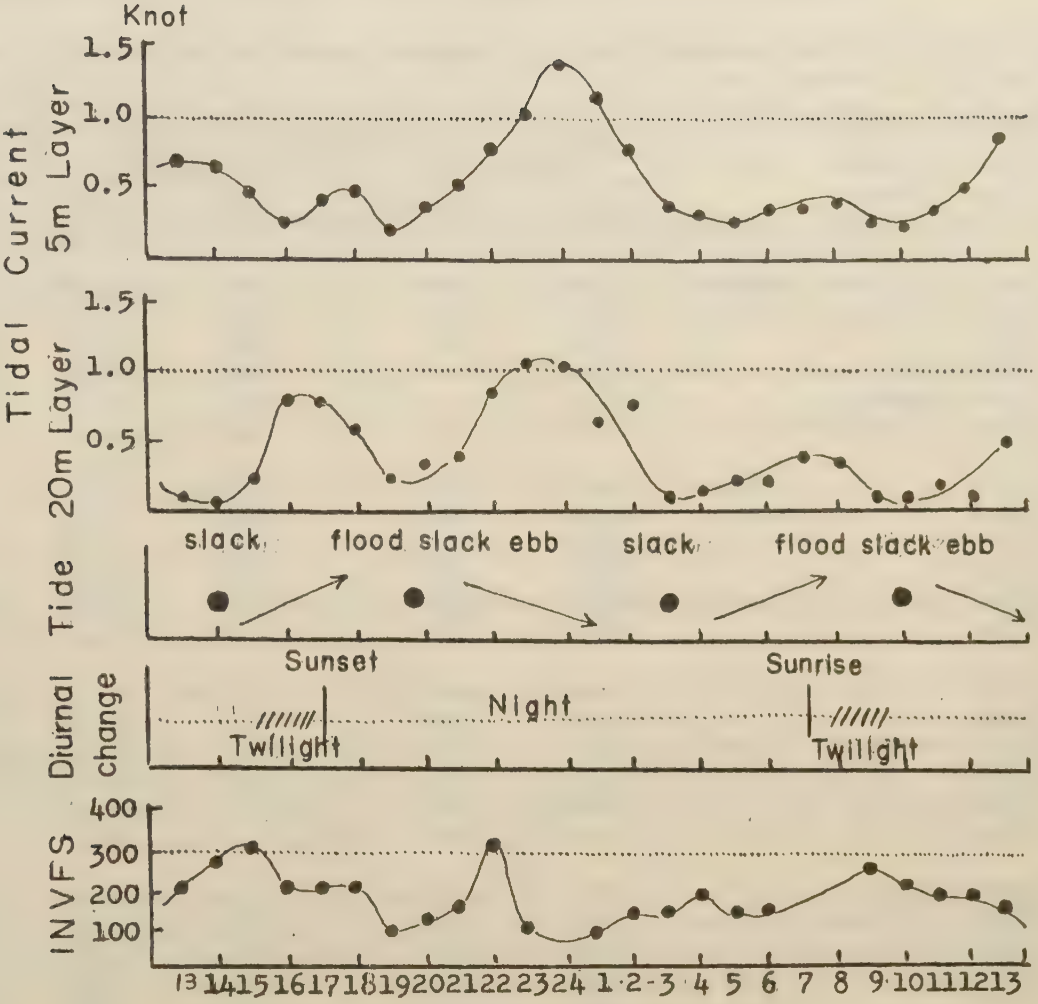

Fig. 8 Condition of fish schools around reef

TABLE I

Diurnal variation of fish schools around the Ebisone

Date	Time (Hrs)	Diurnal change	Tide	Current				INVSF
				Direction*		Speed**		
				5 m Layer	20 m Layer	5 m Layer	20 m Layer	
11 Dec	1300		Slack	220	300	0.65	0.08	225
"	1400	Twilight	Flood	210	***	0.63	0.04	300
"	1500			190	***	0.42	0.22	350
"	1600			190	0	0.21	0.76	225
"	1700	Sunset		30	0	0.38	0.78	225
"	1800	(1712)		320	20	0.41	0.57	225
"	1900		Slack	180	130	0.17	0.22	100
"	2000		Ebb	250	160	0.39	0.31	130
"	2100			270	230	0.49	0.34	175
"	2200			200	210	0.75	0.85	350
"	2300			220	210	1.02	1.04	100
"	2400			220	220	1.42	1.03	****
12 Dec	100			220	210	1.13	0.61	100
"	200			220	200	0.74	0.78	150
"	300		Slack	220	160	0.36	0.09	150
"	400		Flood	120	***	0.32	0.14	200
"	500			300	80	0.25	0.19	150
"	600			50	***	0.34	0.17	150
"	700	Sunrise		60	40	0.31	0.34	****
"	800	(0715)		60	30	0.37	0.30	****
"	900	Twilight		20	***	0.26	0.09	275
"	1000		Slack	290	320	0.22	0.05	225
"	1100		Ebb	250	***	0.31	0.15	200
"	1200			230	***	0.50	0.06	200
"	1300			200	230	0.86	0.48	175

* Magnetic compass bearing by degrees
** Mile/hour
*** The magnetic box out of order
**** The fish-finder out of order
Age of the moon: 11 Dec 13.9 days
12 Dec 14.9 days

3 · DIURNAL VARIATION OF FISH SCHOOLS AROUND REEFS

Observations were made on the dirunal variation in the formation of fish schools around natural reefs to ascertain its relation to tide and sunlight.

Day and night observations were carried out at Ebisone, outside Nagasaki Port, surveying the fish schools every hour with echo fish-finders operated in eight directions from the buoy which was set at the centre of the fishing bank. At the same time, on another boat, anchored 60 m south-west of the buoy, current observations were carried out at 5 m and 20 m layer depths.

Figure 7 shows the distribution of fish schools around Ebisone at hourly intervals.

The index number of the volume of fish school (INVFS) by echonograph, was as follows:

$$P = (1 \times n_1 + 2 \times n_2 + 3 \times n_3 + \ldots\ldots)/(n_1 + n_2 + n_3 + \ldots\ldots) \times 100$$

P .... Index number of volume of fish school (INVFS)

1, 2, 3, ... Ranks of fish school density

n_1, n_2, n_3 . Number of times of appearance in each rank

The rank of a fish school is computed by multiplying the record mark dimension of fish school by the density of its marks.

The results of these observations are shown in Table I and Fig. 8.

The value of INVFS was related to current and sunlight. The value of INVFS was highest between slack water and half tide. At slack water, the fish school became thinner. About 1 to 2 h before or after slack water, the index number rose to the maximum. The fish school was thicker in swift current than in slow currents.

In slow tidal current, the fishes make flocks above 2 to 3 m from the front part of the peaks on the fishing bank or scattered rocks around the bank. When the current becomes strong, they come together in front of the highest peak above 2 to 3 m. At night the fish school keeps close to the bank side slope and when the current becomes swifter the fishes swim up above 2 to 3 m from the slope.

When the sun's altitude has set in 20 degrees or less above the horizon, the intensity of underwater illumination goes down. In the twilight that comes before sunset and after sunrise, the fishes concentrate in the sea. From 2 to 1 h before sunset and from 1 to 2 h after sunrise, the fish schools are situated above 5 m from the highest peak of the fishing bank, and are the thickest observed.

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